Novel measures to investigate the social structure and reproductive performance in a dynamic sow herd using social network analysis

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A thesis submitted for the degree of Doctor of Philosophy (PhD)

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Submitted for examination September 2020

Abstract

The transition from stalls to group housing has increased agonistic behaviours, with a detrimental impact on welfare and productivity. Understanding social behaviours is pivotal for improving welfare and extensive research has aimed at reducing aggression. Recently, there has been a shift in perspective to consider the impact of socio-positive interactions on the welfare of captive species. The complexities of how individuals impart positive or negative effects require a technique that transitions to a group-level. Social network analysis (SNA) has developed as a valid technique in animal behaviour, although comparatively few studies have focussed on commercial animals. Understanding the stability of behaviour enables predictions of future behaviour to be made, which could inform management strategies. This thesis investigated the social structure of a dynamic breeding sow herd as a model species in preferential association and agonistic networks over three production cycles. Preferential associations refer to the lying behaviour < 1m from selected partners. The study examined the impact of individual behaviour on network composition, evaluating the stability of behaviour and the effect of social position on reproductive performance.

SNA identified socially prominent and influential sows in every preferential and aggression network. Social prominence refers to a significantly higher degree centrality than conspecifics and social influence refers to a significantly higher betweenness centrality. In the preferential networks, there was an indication of discriminatory selective behaviour towards sows that were more highly connected. Although a lack of reciprocation showed no formation of sustained friendships, indicating alternative motivations for selective interactions. Prominence was not revealed as stable in the preferential association or agonistic networks. By comparison, influence was more stable in the aggression networks. An association was demonstrated between prominence, stillbirths and crushing. Results indicated a relationship between long-term stability of social position and reproductive performance. Finally, the novel approach of implementing brokerage typologies provided a unique perspective on the composition of the networks, demonstrating how sows are transferring aggression within and between identified subgroups.

Publications and conference proceedings

Jowett, S., Amory, J., Barker, Z., Zaleska, B., 2019. Do pigs have friends: The social structure of a dynamic sow herd. Proceedings of The Association for the Study of Animal Behaviour conference: ASAB Easter meeting. York, 3rd – 5th April 2019.

Jowett, S., Amory, J., 2020. The stability of social prominence and influence in a dynamic breeding sow herd: A social network analysis approach. Proceedings of the STEM for BRITAIN competition. London, 9th March 2020.

Jowett, S., Amory, J., 2020. The stability of social prominence and influence in a dynamic breeding sow herd: A social network analysis approach. Proceedings of the Universities Federation for Animal Welfare Science conference. Virtual, 30th June – 1st July 2020.

Jowett, S., Amory, J., 2020. The stability of social prominence and influence in a dynamic breeding sow herd: A social network analysis approach. *Applied Animal Behaviour Science*: 238,105320.

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Acknowledgements

I would like to express my deepest gratitude to my supervisor Dr. Jon Amory, for his continued guidance, advice, and enthusiasm throughout the past four years. His knowledge and experience have guided me through this project, acting as an immense source of support. Jon's belief in me has been extremely motivating; I am profoundly grateful for the teaching opportunities and unequivocal support at conferences and meetings. My sincere thanks also go to my supervisor Dr. Zoe Barker for her support and encouragement, helping to guide me through interpreting the electronic sow feeding data with her ability to translate Italian! Thank you also to Dr. Nicola Blackie for her advice and orientating me with the workings of the pig unit, and to Dr. Bozena Zaleska for her support at meetings in this final year.

This thesis would not have been possible without the help of the staff at the Sturgeon's farm pig unit. Thank you to James for his generosity and interest in this project. James has been an invaluable source of support, always there to answer questions and making time for me in all aspects of the practical work despite his busy schedule, and always with a smile! I am incredibly grateful to Brian for his patience and the countless hours he supported me with the challenging job of spray marking the sows. Thank you also to Charles for kindly helping to 'herd' curious sows.

I am thankful to my friends and family for their faith in me and their unending interest in all things pig related. Thank you to Liz, Farhan, and Sam, for your enthusiasm in my work, the many hours of listening to my ramblings, and sharing my experiences with such positivity during this journey. To Gareth, thank you for sharing your insights into using 'R' and your patience with my many questions; as a fellow student, our chats on the PhD process have been hugely valuable.

Finally, to my husband and parents, words cannot express how your endless support and love has enabled me to keep positive. To Fletcher, thank you for having faith in me to start this process with all the sacrifices it entailed. My deepest gratitude also for your thoughtfulness and good humour in allowing me the space I needed to complete the crucial stages of this thesis during the stressful lock-down. To my Mum, Maureen Lea, you have shown belief in me every step of the way, a constant beacon of love and support, I am forever grateful for all you have done for me. To my dad, David Lea, my 'number-one' fan, I could never express how thankful I am for your advice, patience, and support. Thank you for pushing me forwards through the challenges, and your advice on all things, 'tech', I could never have achieved this without you. My deepest love and eternal thankfulness to you all.

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List of abbreviations

ACTH: ……. Adrenocorticotropic hormone

BMI: …….. Body mass index

B0: …… No brokerage role

B1: …… Coordinator

B2: …… Gatekeeper

B3: …… Representative

B4: …… Consultant

B5: …….. Liaison

GLMM: …… General linear mixed model

E-I Index: …… External-Internal Index

ESF: …… Electronic sow feeder

HCA: …… Hydrocortisone acetate

HPA: …… Hypothalamic pituitary adrenal

PC1: …….. Production cycle 1

PC2: …….. Production cycle 2

PC3: …… Production cycle 3

PPV1: …… Porcine parvovirus type 1

SIS: …….. Socially influential sows

SPS: …… Socially prominent sows

SNA: …… Social Network Analysis

Std error: …… Standard error

Chapter one: Literature Review

1.1. Introduction

In December 2019, the total number of breeding sows in the UK stood at 404,000, representing a £1.6 billion industry (AHDB, 2020). Consumer demands and changes to legislation encompassing commercial pig farming have resulted in an industry-wide increase in dynamic management practices and unfamiliar breeding sow group sizes, currently averaging seventy individuals. Dynamic practices refer to the frequent and continuous removal, and introduction of pig cohorts to the herd. Since 2013, the UK industry ban on sow stalls transitioned accommodation to group-housing (Directive 2008/120/EC). The EU legislation states that sows will be kept in group-housed conditions during gestation until one week before expected farrowing and four weeks after servicing. The implementation of group housing served to improve welfare, allowing for the expression of normal activity and behaviour (Maes et al., 2016). Repeated mixing and highly dense populations of breeding sows create unstable social networks, increasing aggression and contravening the social structure that pigs are innately adapted to (Mendl, 1995). Maintaining social systems is an effective method of enhancing coping strategies and welfare. Robust, species-specific social networks are particularly advantageous for coping with environmental challenges, providing social support from conspecifics (Koene and Ipema, 2014). However, when there is a provocation to homeostasis, costs to sociality occur with detrimental effects upon health, behaviour, reproduction, and wellbeing (Mellor and Beausoleil, 2015). While extensive research has focused on attempting to find a unified solution for reducing the levels of agonistic interactions within dynamic systems, few studies have concentrated on the impact of positive relationships (Durrell et al., 2004). Traditional methods of identifying those at risk or those that promote a

positive or negative effect within a gestating herd typically define individuals as low-ranking, high-ranking, subordinate, or dominant. Utilising predefined, current behavioural and physiological profiles may not reflect an accurate indicator of social status or an individual's impact. There is a need to disentangle the confounding factor of social structure plasticity in dynamic systems, where the temporal social configurations will influence this fluidity in conjunction with individual differences in behavioural reactivity (Hazel and Lloyd, 2016). This thesis will consider a novel method for describing social structure in both positive and agonistic behavioural networks using dry breeding sows as a model dynamic species. It will seek to provide an alternative perspective of individuals that impact the social dynamics and evaluate the stability of individual behaviour over time through the application of social network analysis.

1.2. The social behaviour of pigs

1.2.1. What is sociality?

Gregarious animals depend upon the capacity to engage and interact with their conspecifics over contexts and time to achieve maximum fitness. Social interactions are complex, influenced by a multitude of variables such as group size, social stability, group structure and the diversity of social roles (Hobson et al., 2019). The positive contexts in which sociality and 'working together' aide survival and success both, directly and indirectly, include predator avoidance, resource acquisition, mate acquisition, alloparental care and homeostasis (Hofmann et al., 2014). In contrast, conflict and competition between conspecifics maintain social hierarchy in many species (Hobson, 2020) and is also reflective of individual differences in behavioural reactivity. However, the expression of

sociality is fundamentally determined by the social environment (Silk and Fisher, 2017). It is this manipulated level of social control experienced by captive animals which influence shifts in the social dynamics contrary to what is typically expected in any given species.

1.2.2. The social structure of wild boar

Wild female boar form structured matriarchal groups consisting of offspring and subadults (Gonyou, 2001). Mother-daughter groups are generally stable, despite seasonal changes to the social dynamics occurring between autumn and winter due to breeding (Marchant-Forde, 2010) and variability in food abundance (Bieber and Ruf, 2005). Stability is achieved through an established hierarchy in which subordinates avoid conflict with dominant sows (Gonyou, 2001). Linear rankings and social roles reflect the complex structure where fitness benefits are attained. Forcardi et al. (2015) demonstrated that cooperative behaviour in wild boar is more beneficial than competitive or aggressive behaviour. Also, Forcadi et al. (2015) further described an organised system involving the division of labour within sounders, the term used to describe a social group of pigs. The study found male and female yearlings acting as scouts for foraging sites. Therefore, individuals on the periphery of the social structure provided fitness benefits to all, demonstrating that perceived lower-ranking individuals can have a significant impact on group survival when adhering to a social role. Fundamental to cooperation is familiarity, achieved by visual, olfactory, and auditory cues (Kristensen et al., 2001) either through kin recognition or kin discrimination (Hamilton, 1964). It can almost certainly explain why group size is an essential factor for stability and ultimate success. The sophistication of wild boar social groups and cognition is also displayed in their behavioural flexibility in response to environmental changes or challenges. For example,

unrelated female yearlings can form stable groups in the absence of adult females, albeit with a nonlinear hierarchy (Bieber et al., 2019). Phenotypic variations (i.e., coat colour) that are potentially detrimental to group survival can increase aggression not typically observed in wild herds (Battocchio et al., 2017). Context-dependent personality changes that enhance offspring survival have also been documented (Vetter et al., 2016).

1.2.3 The social structure of commercial breeding sows

The principal contributors to the social structures and behaviours observed in commercial breeding sows are group size, group type, feeding mechanisms and space allocation (Bench et al., 2013a, 2013b). The mean herd size for wild boar in Europe is four, although on other continents, such as Asia, mean herd sizes are generally lower (Guo et al., 2017). In comparison, breeding sows are often housed in large groups >50, consisting of unfamiliar and phenotypically similar conspecifics. At high stocking levels, the strategies of kin discrimination and the maintenance of dominance hierarchies become challenging at group level and therefore, alternative behavioural strategies are implemented. Established research proves that group type influences behaviour; dynamic systems regularly disrupt the social context, engendering an increase in acute agonistic encounters post-mixing as dominance hierarchies are attempted to be reformed (Tönepöhl et al., 2013). However, evidence also suggests that group size may not determine the levels of aggression observed and suggest a negative correlation between aggression and numbers of pigs (Turner and Edwards, 2004; Samarakone and Gonyou, 2009); a pattern of behaviour also documented in domestic fowl (Estevez et al., 2003). The costs associated with attempting to exert dominance in an unmanageable group size becomes unsustainable with an increased risk of injury and potential

infection (Stuckenborg et al., 2011; Clegg et al., 2016). By reducing aggressiveness at an individual level in response to a large social group, these detrimental costs can be mitigated (Andersen et al., 2004). Fundamental to the success of this behavioural strategy is the provision of appropriate space, enabling the ability to avoid conflict and regulate aggression. In comparison to smaller groups, large group sizes may reduce the levels of attack and subsequent injuries (Turner et al., 2001), a result of increased floor space (Weng et al., 1998). Despite the recommendations of 2.25m² per sow from the Red Tractor Assurance guidelines for pigs (Assured Food Standards, 2014), research has still yet to agree on the optimal space allocation for welfare and production, with recommendations ranging from 2.4m² to 9.3m² per sow (Greenwood et al., 2014).

An alternative strategy relates to the formation of subgroups; Gonyou (2001) proposed that when group size does not allow for the construction of linear hierarchies, subgroups will form that avoid conflict with other subgroups. The concept of subgroup formation in commercial pigs is a contentious topic; research has argued that the construction of subgroups based upon preferred lying locations in a restrictive space remains unresolved (Turner et al., 2003; Turner and Edwards, 2004). Subgrouping is a strategy for reducing competition in a large social group, as documented in the foraging behaviour of free-ranging pigs (Rodríguez-Estévez et al., 2010). The study found that during the day foraging subgroups developed, with individuals returning to a united group during evening rest periods. However, it could not ascertain if the subgroups formed during the day consisted of the same individuals and therefore cannot support a theory of selective affiliative relationships but instead demonstrates cooperative behaviour. Despite the disparities between subgrouping studies based upon individual response to a social group at a network level, studies

have shown that pigs can form subgroups under directed management. Premixing sows before introduction into a dynamic herd reinforces subgrouping behaviour after remixing, reducing aggression between subgroup conspecifics and between resident, and new sows (Van Putten and van de Burgwal, 1990; Durrell et al., 2003). Such a technique reveals the kin recognition concept in smaller groups and presents the question of how can a preferential association truly be defined? There are many confounding factors underpinning why sows might choose to be selective with whom they frequently interact. If benefits are to be gained, such as access to a preferred lying location, then although pigs might not have sustainable friendships, they may at the very least be expressing mutual tolerance of selected individuals. Tolerance is a useful trait, and if enacted, it becomes a mechanism for regulating aggression, a social strategy employed by commercial chickens (Abeyesinghe et al., 2013).

1.3. Agonistic behaviours

While voluntary behavioural measures may start with the aim of reducing agonistic encounters, ubiquitous aggression still prevails as the greatest threat to welfare and production surrounding group-housed sows. Acute aggression follows a mixing event during the reestablishment of the social hierarchy. It can occur up to 48 h post-mixing (Meese and Ewbank, 1973), with prolonged aggression persisting in response to competition for valuable resources or aberrant behaviour in a densely populated environment (McGlone, 1986). Despite extensive research, with no unified solutions, this remains an important topic of concern for the industry (Peden et al., 2018). The link

between welfare and production highlights the continued need for developing effective management strategies.

1.3.1. Sociality and agonistic behaviours

Agonistic behaviours are a necessary mechanism for maintaining social structure and cohesion in many species. Pivotal to this cohesion is the formation of predictable and established relationships and hierarchies in which conspecifics know their social role in the group, allowing for conflict escalation to be avoided (Holekamp and Strauss, 2016). Dominance hierarchies are often characterised with the emergence of higher-ranking individuals who achieve elevated social rank determined by their experience, competitive abilities or fighting success (Lea et al., 2014; Büttner et al., 2020). In wild boar, acts of direct aggression are infrequent and of low intensity, with social stability determined by linear, stable hierarchies maintained by threat or displacement behaviour (Schnebel and Griswold, 1983). By comparison, social instability increases aggression in commercial pigs (Tönepöhl et al., 2013), documented in other commercial and domestic animals including dairy goats (Andersen et al., 2008), dairy cows (von Keyserlingk et al., 2008), rabbits (Andrist et al., 2014), horses (Christensen et al., 2011) and domestic fowl (Carvalho et al., 2018). Agonistic interactions classify as threats, aggression, and submission (McGlone, 1986) in the form of direct physical contact or visual and auditory signals. Fight sequences are complex and defined as a continuum of behaviour (McGlone, 1986). Table 1 outlines a comprehensive ethogram of agonistic behaviours in pigs.

Table 1. Ethogram of agonistic behaviours observed in swine, including physical, visual, and auditory interactions. Behaviours are sub-divided into aggression, threats, and submission (McGlone, 1986).

Agonistic behaviour	Description	Author
Aggression		
Parallel pressing	Sows stand side by side and push hard with the shoulders against each other, throwing the head against the neck or head of the opponent.	Jensen, 1980; Jensen, 1982
Inverse parallel pressing	Sows face front to front and push their shoulders hard against each other, throwing the head against the neck and flank of the opponent.	Jensen 1980; Jensen, 1982
Head-to-head thrust	With mouth closed, a rapid thrust upwards or sideways with the head or snout against the neck, head, or ears of the opponent.	Jensen, 1980; Jensen, 1982
Head-to-body thrust	With mouth closed, a rapid thrust upwards or sideways with the head or snout against any part of the body behind the ears of the opponent.	Jensen, 1980; Jensen, 1982
Bite	With an open mouth, the initiator bites the recipient on any part of the body.	Camerlink et al., 2015
Physical displacement	The physical displacement of an opponent from original location through chasing pursuit.	Büttner et al., 2015; Camberlink et al., 2016a
Threat		
Parallel walking	Opponents are walking simultaneously with shoulders next to each other.	Camerlink et al., 2015; Camberlink et al., 2016a
Aiming	An upward directed thrust of the snout directed at the receiving pig.	Keeling & Gonyou, 2001
Vocalisation (grunts)	Short rapidly repeated grunts.	Marchant et al., 2001
Shoulder-to shoulder display	Opponents are standing or walking while contacting shoulder-to-shoulder, without significant pressure.	Camerlink et al., 2015; Camberlink et al., 2016a
Submission		
Retreat	Sow turns and flees from the opponent in response to aggression	Arnone & Dantzer, 1980; Camberlink et al., 2016a
Avoidance	Sow changes direction to avoid a potential agonistic interaction.	McBride et al., 1964; Ison et al., 2010
Rump display	Subordinate sow remains stationary and presents hindquarters to an opponent.	Arnone & Dantzer, 1980,
Vocalisation (squeals)	A signal of submission or fear using a high-pitched squeal.	McBride et al., 1964; Marchant et al., 2001
Head lowering	The lowering of head and eyes by the subordinate sow.	McBride et al., 1964; Jensen and Wood-Gush, 1984

1.3.2. The impact of aggression on welfare

Extensive research has documented the detrimental impact of intra-specific aggression on overall welfare and wellbeing in commercial animals. Chronic hostility can be considered a social stressor. Social stress arising from an unstable and aggressive environment has direct and indirect effects. Welfare is perceived to be in two states; relating to the physiological and psychological impact (Webster et al., 2004; Dawkins, 2004).

1.3.2.1. The physiological impact of aggression

Visual markers are an indication of the unwanted physical welfare of pigs (Welfare Quality®, 2009). Such injuries including lameness, wounds and vulva damage are detrimental to the overall health of the animal, a consequence of associated pain and increased susceptibility for infection. Acute aggression observed in dynamic systems, in which unfamiliar sows are routinely added and removed from the social group, increases the potential for skin lesions (Turner et al., 2006), with lameness and vulva injuries also leading to weight loss and mortality. Lameness is identified as the primary cause of death in pigs; a study in Denmark found that 72% of the unplanned culling of sows was the result of locomotion disorders (Kirk et al., 2005). Lameness can also lead to a reduction in feed intake when the sow becomes less mobile due to pain and increases their lying behaviour (Cornou et al., 2008; Ala-Kurikka et al., 2017). Sequential feeding imposed by electronic sow feeders in group housing also engenders aggression as sows jostle and compete for food, increasing the chance of vulva injuries, skin lesions and lameness. Electronic sow feeders (ESF) are a technology that provides an individual feeding regime that allows each sow to be allocated the specific feed ration for its individual requirements, such as body weight (Olsson et al., 2011). The

technology also monitors health, for example, the system records if an animal feeds daily and how much of their allocated feed has been consumed. In addition to the visual indicators, stressors brought about by social instability, large groupings, and aggression detrimentally impact biological processes (Bartolomucci, 2007). Prolonged social stressors create homeostatic imbalance resulting from changes in neuroendocrine activity, influencing immunity, disease susceptibility and metabolic responses (de Groot et al., 2001; Proudfoot and Habing, 2015; Chebel et al., 2016). The exposure to social and environmental stress is an established link to production, negatively affecting meat quality and tenderisation in both pigs and beef cattle (Rubio-González et al., 2015; Díaz et al., 2020). Table 2 provides examples of the extent to which social stress imparts deleterious effects upon health in commercial species.

Table 2. Examples of the impact of aggression and social stress on the physiological state in commercial species.

Species	Health issue	Authors
Pigs	Gastric ulcers, vulva injuries, skin lesions, lameness	Kirk et al., 2005; Turner et al., 2006; Cornou et al., 2008; Holinger et al., 2018a
Chickens, fish, lambs, pigs	Increased vulnerability to disease	Conte, 2004; Alpigiani et al., 2017; Galapero et al., 2015; Tuchscherer et al., 2018
Chickens, cows, pigs	Immune dysfunction	Matur et al., 2015; Chebel et al., 2016; Schalk et al., 2018
Dairy cows	Mastitis	Holtenius et al., 2004
Dairy cows, fish	Reduced growth rate	Fernandes-de-Castilho et al., 2008; Fiol et al., 2017
Pigs	Adipose tissue development	Holinger et al., 2018
Dairy cows	Uterine disease	Proudfoot et al., 2018
Fish	Scale loss	Laursen et al., 2013

1.3.2.2. The psychological impact of aggression

Psychological wellbeing comes from the balance of homeostasis between internal cognitive mechanisms and the external environment. The effects of aggression on mental wellbeing are more complex than the physiological impact due to individual differences and context-dependent responses, making the emotional state more difficult to assess. Psychological wellbeing is considered as two fundamental areas; firstly, can the animal perform naturally occurring behaviours and secondly is the animal absent from fear and distress. Abnormal behaviours are typically associated with a low emotional state, influenced by a restrictive and unenriched environment rather than aggression or social instability. These displays of behaviour manifest in many commercial species including feather-pecking in poultry, tail-biting in pigs, tongue-rolling in cattle and fur-biting in mink (Blokhuis and Arkes, 1984; Redbo, 1992; Jensen et al., 2010; Malmkvist et al., 2013). However, since the ban of sow stalls where stereotypical behaviours such as bar and trough biting were commonplace, gestating sows in group housing systems do not perform these evident displays of distress. These detrimental qualities continue to occur in the farrowing crates, where sows are confined (Zhang et al., 2017). Furthermore, recent research has documented the impact of long-term moods derived from contest outcomes on future aggressive interactions (Crump et al., 2020), further highlighting the importance of emotive state, derived from the social environment, on individual decision-making and subsequent expression of behaviour.

Aversive husbandry tasks in commercial farming are routine and dynamic systems induce unpredictable social environments. Assessments of fear behaviour have traditionally been achieved through the open arena, novel object approach or restraint tests. Nonetheless,

evaluation of these traditional tests has indicated that they lack validity to measure fear due to a lack of correlation between tests and habituation effects over time (Forkman et al., 2007; Murphy et al., 2014). More recently, cognitive bias highlights as a more useful measure of emotion, mood, and fear, wherein individuals with a negative affective state will make pessimistic decisions (Murphy et al., 2014; Carreras et al., 2016). Cognitive bias is described as the effect of emotional state on cognitive processes including decision making, attention, learning, and memory recall (Mendl et al., 2009). A negative emotional state in pigs is already associated with an increased frequency of skin lesions, indicative of injuries through aggressive encounters, compared to individuals with a positive affective state (Carreras et al., 2016). Although the expression of aggression is ubiquitous in gregarious species, a mechanism for maintaining social order in certain groups, the evidence clearly shows that continued exposure to social stressors such as aggression is detrimental to emotional wellbeing.

Unlike the stable social networks of wild boar, in which groups are smaller, familiar and consist of a defined hierarchy, commercial sows experience unstable social conditions, with large groupings, unfamiliar conspecifics and the regular removal, and addition of individuals. In these unstable behavioural networks of group-housed sows, it might be expected that social status would play an essential role in emotional responses to aggression and subsequent mental health; however, the evidence provides contradictory results. An investigation into the emotional state of pigs used the Qualitative Behaviour Assessment to determine emotional response after an agonistic interaction; results showed no significant differences between the arousal or valence of winners and losers (Camerlink et al., 2016b), an effect demonstrated in other species (Earley et al., 2006). These

findings are further supported by previous studies which found no differences in cortisol concentrations between subordinate and dominant pigs (Tuchscherer et al., 1998; Rudine et al., 2007). The hypothalamic-pituitary-adrenal axis produces cortisol during periods of stress (Turner et al., 2005). Therefore, irrespective of social standing, different individual coping styles in response to environmental challenges such as aggression may determine emotional wellbeing at an individual level (O'Malley et al., 2019). For example, the mechanisms employed by an individual to cope with social and environmental challenges are established by many confounding factors, including age, experience, behavioural flexibility, and the social context.

Behavioural responses are a useful mechanism for identifying psychological stress and anxiety (Temple et al., 2011) with qualitative behavioural assessments and free choice profiling approaches previously applied in welfare research (Wemelsfelder et al., 2000; Rutherford et al., 2012). Additionally, the welfare quality assessment protocol for pigs (Welfare Quality®, 2009) provides an objective evaluation system of emotional state for practitioners with a criteria of positive state measurement through the application of terms related to expressive attitudes such as happy, relaxed, content, or indifferent. Although perceptions of emotional state are subjective and open to misinterpretation, these measures of emotional state are considered reliable and valid (Rutherford et al., 2012; Wemelsfelder and Mullan, 2014). However, to fully comprehend the extent to which aggression is imparting detrimental effects at a group or individual level, the observer must recognise that agonistic behaviours are occurring and impact on welfare. Peden et al., (2019) supports this argument in a study that highlighted the time when aggression was observed influenced welfare opinions. The study found that when observing video footage of pigs

during and after fighting, there was a disparity in the perceptions of welfare. Farmers who only observed the aftermath of fighting injuries deemed the injuries to be less severe than farmers who directly witnessed fighting behaviour. Farmers are vital in implementing intervention and management strategies to reduce aggression, and therefore, their perceptions of aggression are critical. A recent study found a substantial disparity in the stage of production in which farmers perceived hostility as a problem, with 73% believing that aggression during weaning was not considered a welfare issue. Although ear, tail, and flank biting are typically not the result of aggression *per se*, the study assessed aggression by these visual indicators including ear and found only 16% of farmers expressed concern about animal stress based on these observations (Camerlink and Turner, 2017). As such, the divide between welfare scientists and farmers highlights the need for a measure of aggression at both group and individual level that can extend upon subjective observations to bridge the gap between perception and reality. Specifically, when focussing on the impact on the less tangible issue of emotional welfare.

1.3.3. The impact of aggression on reproductive performance

In addition to the chance of injury, disease, infection, and reduced immunity associated with agonistic interactions, receipt of aggression elevates exposure to social stress. Chronic exposure impairs reproductive performance as the hypothalamic-pituitary-adrenal (HPA) axis becomes activated. With the activation of the HPA axis, stress hormones are released that reduce the levels of the reproductive hormones; gonadotropin-releasing and luteinising hormones required for successful estrus and ovulation (Lucy et al., 2016). Although it is generally accepted that stressors impair the reproductive performance, it has been argued that how an individual copes with social

challenges can increase or reduce the impact of stress. Turner et al. (1999, 2005) propose that acute and repeated acute stress does not impact endocrine processes, with some pigs also resistant to the effects of chronic stress. As with the emotional state, research continues to demonstrate that individual differences are pivotal for determining the impact of challenges on any given animal. Despite this, there are a proportion of animals that will continue to be detrimentally affected. The link between welfare and production highlights the continued need for developing effective management strategies during gestation. There are four crucial areas of the reproductive processes that are impacted upon through stress exposure, such as aggression, during gestation including, foetal development and mortality, neonatal mortality, maternal behaviours, and postpartum piglet development.

1.3.3.1. Piglet development and mortality

Numerous multifactorial variables increase the chance of stillborn piglets which include factors relating to the sow, the environment, duration of farrowing time and genetics (Vanderhaeghe et al., 2013). However, elevations in the frequency of stillborn and mummified piglets are also positively correlated with stress during gestation (Cronin et al., 1996). Despite extensive research, stillborn piglets continue to represent significant welfare and economic concern, accounting for an average of 8% of all piglet mortality rates (Vanderhaeghe et al., 2010b). Supporting the proposal of chronic stress impacting upon the reproduction (Turner et al., 1999, 2005), studies have shown that exposure to fear-related stimuli 16-18 days postpartum increases the chances of stillborn piglets more significantly than exposure only 2-4 days before farrowing (Hemsworth et al., 1990; Hemsworth et al., 1999). As legislation suggests that sows should be moved to farrowing

accommodation approximately one week before parturition (EU Council Directive 2001/93/EC, 2001), this indicates that fear or stressors during the group housing phase of production may be greater than fear associated with the farrowing environment. Although, individual differences in stress response will influence reproductive success and overall health; at a group level, low ranking sows are at significantly higher risk of stillborn piglets than higher-ranking animals (Hoy et al., 2009a). Thus, highlighting the need to implement a measure that identifies sows most at risk within group housing systems.

Piglet immunity is pivotal for protection against diseases; passive sow immunity is crucial for the development of intrauterine antibody formation in foetuses (Vigre et al., 2003). The serological status of the sow is directly controlled by the neuroendocrine system, which in turn, is detrimentally impacted upon by social stress as plasma cortisol concentrations negatively affect blood immune cell development (Engert et al., 2017; Schalk et al., 2018). Disruption to cellular development in foetal piglets is positively correlated to prenatal stress levels (Tuchscherer et al., 2002). Research has also documented the longevity to which piglet immunity can be compromised. Couret et al. (2009a) found that repeated remixing of unfamiliar pigs during late-stage gestation suppressed the efficiency and number of the blood immune cells in piglets up to two months old, with additional reduced adrenal gland weight in piglets of mothers exposed to social stress. A further study documented that the administration of adrenocorticotropic hormone (ACTH), the cortisol inducing hormone, during gestation, significantly increased the numbers of piglet diseases, with 78 % of piglets of ACTH sows contracting a disease compared to 36% of piglets from the sow control group (Otten et al., 2007). Maternally derived antibodies also determine the antiviral

immune response in piglets, affecting vaccination efficiency (De Groot et al., 2007; Fablet et al., 2016). Immunity is particularly vital in a piglet's ability to be protected against mortality-impactful diseases such as porcine reproductive and respiratory syndrome viruses and *Escherichia coli,* whilst also increasing protection against chronic and painful ailments such as arthritis (Lauritsen et al., 2017).

In addition to the impact of prenatal stress on sow and piglet immunity, the effects are far-reaching in piglet development both behaviourally and physically with preweaning deaths representing a high proportion of piglet mortality rates (Mellor and Stafford, 2004; Quesnel et al., 2008). Low piglet birth weights have been documented to be associated with social stress experienced by sows during gestation (Haussmann et al., 2000; Kranendonk et al., 2006b). However, the relationship remains inconsistent due to conflicting results of other studies where prenatal stress has also demonstrated either no effect on birth weight or even increased it in some cases (Merlot et al., 2013). Such inconsistencies may arise from the time when prenatal stress occurred, with differences between the long-term effects of stress during early gestation compared to the later stages of pregnancy (Couret et al., 2009b). Despite these inconsistencies in birth weight, it is acknowledged that prenatal stress can suppress piglet weight gain indirectly. From birth until weaning piglets are entirely dependent on the nutrient and immunity provision of colostrum, with any challenges to the quality, quantity, or composition of colostrum detrimental to piglet health, development, and thermoregulation (Le Dividich et al., 2005; Devillers et al., 2011). For example, chronic stress affects the levels of glucocorticoid hormones and progesterone when the activation of the HPA axis is prolonged and cortisol levels remain high (Beaulieu-McCoy et al.,

2017). As such any changes to the regulation of hormones involved in the production of colostrum will be impactful; an example is a process of lactogenesis in colostrum production being fundamentally controlled by the hormones; progesterone, prolactin, glucocorticoids, insulin, and growth hormones (Szyndler-Nędza et al., 2020). If cortisol concentrations are released during the process of lactogenesis then the immune function of the individual can be detrimentally affected (Aleri et al., 2016), further impacting upon the quality and content of colostrum. Tuchscherer et al., (2002) clearly demonstrated the link between prenatal stress in sows and lowered immune function in offspring, revealing a significant reduction in serum immunoglobin G concentrations and lymphocyte proliferation in suckling piglets from prenatally stressed mothers.

While environmental conditions may assist in enabling piglets to cope both physically and psychologically with the challenges of intensive farming, such as piglet creep areas or enrichment, coping strategies can become compromised by adverse behavioural changes. Animal handling is a necessary process as piglets are routinely involved in husbandry procedures. Although individual differences may influence how an animal responds or is affected by novel experiences, neonates of prenatally stressed sows will be at a welfare disadvantage. Backus et al. (2013) found increased anxiety in piglets of prenatally stressed sows when exposed to a novel arena and social confrontation test, a result also reflected in piglet responses in an open field and novel object tests (Otten et al., 2007; Kranendonk et al., 2007). High HPA axis activation was reported in the offspring of sows stressed by social remixing during gestation and in those sows injected with ACTH during pregnancy (Haussmann et al., 2000; Jarvis et al., 2006). Thus, the reactions of piglets from prenatally stressed sows to challenging or novel situations may be predetermined by compromises

to cognitive development they experienced *in utero*, further heightening piglet fear and anxiety responses (Otten et al., 2010).

A behavioural expression is a central component of social learning and survival in gregarious species. However, prenatal stress in sows can interrupt the development or presentation of such behaviours in offspring. Among these impairments, vigilance, a necessary survival behaviour in wild boar, is shown to be negatively affected in piglets of prenatally stressed sows (Rault et al., 2013). Play behaviours, integral drivers of social learning, and universally accepted as behaviours indicative of wellbeing and positive state, are also detrimentally changed (Boissy et al., 2007; Held and Špinka, 2011; Mintline et al., 2013). Consideration of the effects of prenatal stress on piglet play behaviour is important as a recent study found the offspring of sows exposed to mixing stress displayed reduced exploration, locomotion play, fighting play and mounting behaviour than offspring from control treatment sows (Brajon et al., 2017). A reduction in play behaviours may also be indicative of a negative emotional state (Kranendonk et al., 2006a), in both piglets and other species including fawns, lambs, foals, and calves (Muller-Schwarze et al., 1982; Thornton and Waterman-Pearson, 2002; Cameron et al., 2008; Krachun et al., 2010). Although play fighting is essential for future confrontations (Weller et al., 2019), failure to engage in this aspect of social learning may lead to increased aggression in later life. Kranendonk et al. (2006a) investigated the effects of administering hydrocortisone acetate (HCA) on sows during three stages of gestation. The study found that offspring from the placebo sows engaged in significantly more non-aggressive encounters than offspring of HCA sows. The timing of HCA administration also influenced offspring behaviour, with piglets of mothers dosed at 51-80 days after insemination considerably more

aggressive than their conspecifics. The time when prenatal stress occurs is an indicator of when detrimental changes to the foetus can happen and are documented in numerous studies (i.e., de Groot et al., 2007; Couret et al., 2008; Couret et al., 2009b; Otten et al., 2010), guiding optimum management strategies and interventions. Research shows that with the ability to intervene and potentially reduce negative effects on offspring from prenatally stressed sows, it becomes necessary to identify sows at risk. However, predicting sows most at risk requires an approach that enables the identification of those individuals, a challenging task in large group housing systems.

1.3.3.2. Sow maternal behaviour

A principal determinant of piglet survival postpartum is the maternal behaviour and responsiveness of the sow. Crushing and flopping actions of the mother present a deadly threat to piglets, particularly during the first few days of life. Despite extensive research, crushed piglets continue to be a leading cause of welfare, and economic concern. Increased posture changes during and after farrowing enhance the probability of crushing mortality (Edwards et al., 1986). As prenatally stressed mothers engage in significantly higher levels of posture changes during this time (Rutherford et al., 2014), maternal responsiveness is crucial. The first minute of crushing is a critical period for the sow to shift position, with a 42% mortality increase if the sow fails to transition after four minutes (Weary et al., 1996). However, prenatal stress reduces response latency to some piglet vocalisations, as documented in the Ringgenberg et al. study (2012). Sows were exposed to social mixing stress to investigate the influence of adverse treatment on maternal behaviours, the findings showed a positive correlation between levels of social stress and response time to piglet distress calls. Although the study found no differences in the reactions between

prenatally stressed and control sows during piglet distress tests, prenatally stressed sows spent more time away from the nest. The study also showed that the resting position of sows impacts upon piglet survival. Prenatally stressed sows spent less time in lateral recumbency (sow lying on her side), inhibiting colostrum access and more time in ventral recumbency (sow lying on her abdomen); a position positively correlated to crushing rates (Wischner et al., 2009). Crushing rates increase when high levels of ventral recumbency initially occurs after a sow lies down due to ventral-lateral posture changes (Weary et al., 1998; Marchant et al., 2003). The absence of a definitive relationship between prenatal stress and piglet distress responses may be indicative of the limitations of the test, rather than genuinely reflective of sow responsiveness, as inconsistencies are documented between studies including variables such as genotype differences, parity, experience, or habituation (Andersen et al., 2005; Held et al., 2006; Lensink et al., 2009). The evidence suggests that crushing rates are a good indicator of the impact of prenatal stress on maternal behaviour but driven by posture changes rather than responses to distress vocalisations. The findings of the Rutherford et al. study (2012) also highlight the influence of prenatal stress on maternal care capacity; piglet-directed behaviours are an additional component for offspring survival and the abnormal attention documented in prenatally stressed sows (Rutherford et al., 2014) potentially enhances the chance of piglets being savaged.

1.4. Affiliative behaviours

Extensive research has focussed on reducing negative behaviours in commercial pigs to improve welfare and reproductive performance. By comparison, the impact of management strategies determined by our understanding of the effects of positive actions has received little attention

(O'Malley et al., 2019). It is particularly true in pigs and presents an opportunity to explore welfare from a new perspective. While the repertoire of prosocial behaviours between species is vast, behavioural categories generally include caregiving, affiliation, sharing, social teaching and cooperation (Rault, 2019). There may appear to be costs to the individual regarding specific prosocial behaviours such as sharing and caregiving. When looking from a socio-biological perspective, the subject as well as the recipient benefits from prosocial behaviours. This may ultimately benefit the social group, but the driver is the fitness benefits to the actor, not to the whole group.

1.4.1. Positive directed behaviours: The importance of the nose

Pigs do not engage in the traditional reciprocal positive behaviours typically observed in mammals, defined as allogrooming, although there is an ongoing debate that free-ranging pigs do engage in mutual grooming at a young age (Gonyou, 2001). Allogrooming is an essential mechanism for maintaining social cohesion and stability in other species (Šárová et al., 2016). Pigs do, however, employ a repertoire of positive behaviours that have benefits, although the reciprocal benefits that extend beyond reinforcing familiar ties remain unclear. Social nosing in pigs is one behavioural process enabling the expression of sociality, existing as a parallel for the positive grooming or licking behaviours in other species. The beneficial effect of receiving a positive action is notable in dairy cattle and horses where licking imparts a calming effect on passive partners (Feh and de Maziéres, 1993; Laister et al., 2011). Likewise, in pigs, there are direct benefits of receiving gentle social nosing on growth rate in finishing pigs (Camerlink et al., 2012). Just as negative behaviours regulate cortisol production, as previously discussed, affiliative behaviours can regulate the

production of the neuropeptide oxytocin (Finkenwirth et al., 2015), which in turn is positively correlated to growth rates in rats and bone formation in rabbits (Uvnäs-Moberg et al., 1998; Altay et al., 2020). The relationship between weight and oxytocin is detailed in human research, with a positive correlation between oxytocin levels and BMI scores (Skinner et al., 2019). Interestingly, this may present an explanation for the observations found in animal studies, as oxytocin is involved in the processes of appetite regulation. In addition to the effect of oxytocin on weight, there is reason to consider that social grooming assists in reducing parasite numbers. Parasites may inadvertently affect appetite and subsequent weight gain or loss. While grooming may reduce outbreaks, this would not be the case in commercial pigs.

Social nosing is another indicator of a positive affective state. A recent study identified the relationship between nosing behaviour and emotional state (Reimert et al., 2017). The pigs were subjected to favourable treatments consisting of an enriched environment or adverse procedures involving social isolation. After the trials, positively treated pigs engaged in higher rates of nasal-nasal contacts than those whose experiences were unfavourable. More interestingly, the pen mates of those exposed to both treatments, who were not exposed themselves, were also affected by the treatment type of their conspecifics, indicating a form of emotional contagion and either reducing or increasing nasal contacts accordingly. It demonstrates the value of positive directed behaviours through the nose-to-nose contact as an indicator of welfare at both individual and group level. Although observations must be treated cautiously as reductions in positive interactions can also be indicative of poor health (Stockmaier et al., 2018). When applied to intensive farming practices, these findings also demonstrate how prosocial behaviours could be

compromised by negative emotional states in a dynamic system, when sows are remixed back into the herd. If sows are returning to the herd in a negative emotional state, it may suppress the levels of nasal contacts required for reintroduction through olfactory measures. It follows then, while nosing is not associated with aggression or dominance in pigs (Camerlink and Turner, 2013), any compromises to the expression of this behaviour may indirectly increase aggression in dynamic herds.

1.4.2. Preferential associations

The concept of preferential association and social bonding is founded upon social discrimination between conspecifics. Unlike social support or buffering, that may be context dependant (Rault, 2012), preferential associations will exist when one conspecific may be preferable over another despite the social context, demonstrating different motivations for behaviour. The value of preferential associations in terms of welfare and reproductive success is recognised in numerous wild species. Social bonds increase the numbers of offspring sired by male Assamese macaques, *Macaca assamensis*, (Schülke et al., 2010), improve reproductive success in female humpbacked whales, *Megaptera novaeangliae*, (Ramp et al., 2010) and increase egg production in brown-headed cowbirds, *Molothrus ater*, (Kohn, 2017). Formation of bonds also improves offspring survival, as demonstrated in wild horses, *Equus caballus*, (Cameron et al., 2009), yellow baboons, *Papio cynocephalus*, (Silk et al., 2003) and chacma baboons, *Papio ursinus*, (Silk et al., 2009). However, despite the benefits of positive associations, there is currently little understanding of behavioural effects on commercial animals that could present as a predictor of future reproductive success (Rault, 2012). Increasing fitness benefits through positive association can be perceived in

relationships influenced by homophily effects. In wild boar herds, individuals with lighter coat colours, a result of hybridisation, are often the recipients of intense aggression by their darker-coated counterparts; darker-coated boars correspondingly, show little aggression towards each other. It has been hypothesised this behaviour occurs due to a lighter coat increasing the chance of predation, putting the entire herd at risk (Battocchio et al., 2017). Some affiliative selections may be constrained by the stage of production in which pigs are housed. For example, animals will generally be housed with conspecifics of a similar age; despite other accessible traits being preferable to incite bonding behaviour, such as size, parity, experience, or temperament.

Identifying preferential associations within a social group is necessary to determine structure and stability. During a five-year study in semi-wild cattle, Reinhardt and Reinhardt (1981) found long term bonds, leading to a cohesive and stable social structure. Dorset horn sheep also consistently form multiple subgroups in a herd, consisting of non-random grazing partner selections (Arnold et al., 1981). Where preferential associations form subsequent subgroups and dyads, these will alter the density of a social network, as individuals are selecting with whom they associate. For example, in a wild boar herd, it is expected that density in an aggression network would be low, as agonistic interactions are rare (Stolba and Wood-Gush, 1989). In contrast, density in an affiliative or preferential association network would be high and consistent. While preferred partners were identified in commercial pigs (Peterson et al., 1989; Jensen and Stangel, 1992), probably kinship and stage of development were influencing factors when assessing the development and stability of social bonds. In the Jensen and Stangel study (1992), pre-weaned pigs in a semi-natural environment displayed a preference for the mother to be their nearest neighbour while engaging

in either active or lying behaviour, although, after weaning, this preference altered to a littermate. It is an association shift also observed between mother and offspring in free-ranging Scottish hill sheep and bison (Green et al., 1989; Lawrence, 1990). Characterising preferential associations based upon parental-offspring relationships, the formation of social bonds with littermates or in stable social networks may not fully explain the motivations involved in social bond establishment between unfamiliar and unrelated conspecifics in dynamic groups.

Dynamic social systems in commercial farming are reflective of fission-fusion societies observed in the wild. In these fission-fusion societies, despite temporal instability in social structure and dynamics, stable and long-term preferential relationships are seen, even between unrelated conspecifics (Möller et al., 2001; Carter et al., 2013). In captive animals, it is proposed that social discriminations occur due to more altruistic reasons, in which preferred conspecifics become selected for traits that aide development, learning and coping strategies in stressful situations (Levengood and Dudzinski, 2016). This perspective gives greater meaning to the findings of the Durrell et al. (2004) study, which investigated preferential associations between unrelated pigs that had experienced remixing events. Unlike the previous pig studies (i.e., Peterson et al., 1989; Jensen and Stangel, 1992), this was the first study to reflect behavioural responses in an environment that involved dynamic practices. The results showed that the establishment of preferential associations remained inconclusive due to the confounding factor of preferred lying locations. Although 97% of pigs appeared to engage in preferential associations in the first mixing event, only 36% of the same pigs repeated preferred lying behaviour with the same conspecific in the second mixing event. The study demonstrates the importance of repeated observations to

ascertain the continuity of conspecific-directed activities. It also highlights the need to apply thresholds in preferential association studies to differentiate between non-random encounters and random actions motivated by other social processes or preferences (i.e., Boyland et al., 2016; Davis et al., 2018). Although threshold filtering is a technique employed for proximity data rather than direct observations, it is an essential element of consideration in the formation of data collection techniques to overcome the limitations of preferential association studies. The use of behavioural thresholds is further supported by Farine (2015a), who states '*a lack of correlation between proximity and interaction networks could arise because they capture fundamentally different social processes'*. As such, social tolerance may confound preferential association studies, particularly in environments that are densely populated with spatial constraints, as highlighted in the Abeysinghe et al. (2013) research of laying hens. The study investigated the dyadic preferential associations of Hyline Brown pullets housed with unfamiliar conspecifics but did not support the hypothesis that hens had friends. Associations did not remain across time, active space use or perching contexts when conducted under experimental conditions with a small number of hens housed in a confined space, eight hens housed in a pen of 3.1m^2. The inconsistencies in preferential association research and the confounding factors highlight the continued need to investigate these potentially welfare-improving relationships among commercial pigs. Further, addressing the unanswered question of the temporal stability of relationships in dynamic systems.

1.4.3. Social support

In contrast to preferential associations, social support is a mechanism employed by animals to reduce the impact of negative and challenging experiences. The benefits arise from the physical presence of conspecifics, where familiarity is not necessary for support to be accessed (Tokumaru et al., 2015) unlike the discriminatory affiliative relationships and direct affiliative interaction associated with preferential associations. The concept of rewarding behaviour is defined as either a main or direct-effect or buffering-effect (Cohen and Wils, 1985). The main or direct-effect model suggests that social support acts to maintain homeostasis even in the absence of any potential environmental or social challenge. By comparison, social buffering is more context-specific, with the behavioural mechanism only employed in response to a direct threat or stressful event. Examples, of main and direct-effect support in animal societies, may originate from maintaining cohesion together with stability through specific behaviours, engendering predictable social environments. Nevertheless, in dynamic, commercial species, this model of social support is challenging to achieve. Social buffering is a more appropriate model to evaluate group-housed sows, with the potential to reduce indicators of negative experiences including, distress behaviours, HPA axis activation, heart rate and immune response (Rault, 2012), by lowering corticosterone levels (Mikami et al., 2020).

Social buffering promotes enhanced welfare by reducing fear responses; with examples documented in numerous species. Sheep exposed to social isolation tests demonstrate increased activity and escape behaviours (González et al., 2013) with dairy calves nursed by their mothers showing lower heart rates in a novel-object test compared to calves separated from the mother 24

hours after birth (Buchli et al., 2016). The presence of the mother during aversive stimulus treatments of offspring also reduces negative behavioural responses in chicks (Edgar et al., 2015). Mitigating negative responses to unfamiliar and aversive events through social buffering provides an opportunity for management strategies to be employed that alleviate the species-specific stress responses to routine farm practices. The greatest threat to homeostasis in gestating sows is the frequent addition or removal of individuals from the herd, and subsequent social unpredictability and increased aggression. Premixing unfamiliar sows will encourage the development of subgroup solidarity after re-joining the herd, reducing aggression amongst subgroup conspecifics and between resident, and new animals (Durrell et al., 2003), possibly due to avoidance behaviour. It must be noted that the benefits of premixing may become compromised by the replacement rate of sows and the size of the remixing group (O'Connell et al., 2004). Also, the presence of a familiar conspecific is observed to reduce the detrimental effects of social defeat; social isolation proceeding a social defeat prolongs HPA activation in gilts (Ruis et al., 2001). With increasing research into the personality styles, the benefits of social support can also be compromised by temperament and are a further consideration for management techniques. Ruis et al., 2001 highlights the effects of individual coping styles, the study found that stress responses to isolation differed in intensity and duration between active and reactive copers. During isolation, gilts were unable to see littermates, but were able to hear their vocalisations, providing a level of social support. Active copers demonstrated higher rates of exploratory behaviour than passive copers during isolation and recovered from isolation stress more rapidly as documented by body temperature. During isolation active copers had a lower parasympathetic response to novelty than passive copers, suggesting that passive copers find novel challenges more stressful.

1.5. Social roles in animal networks

Animal social networks are complex, influenced by the diversity of species-specific social interactions, environment, and individual differences. Like humans, gregarious animal societies require stability to enhance fitness, survival, and reproductive success, achieved through social organisation (Hobson et al., 2019). Some species have clearly defined social organisation and roles such as in eusocial species where specific behavioural characteristics or capabilities are predetermined at birth, i.e., Damaraland mole-rats, *Fukomys damarensis,* and bees, *Bombus impatiens* (Kelley et al., 2019; Starkey et al., 2019). Other species demonstrate plasticity in social structure, where social roles are not inherently predetermined so are achieved and maintained through other means (e.g., primates, Tombak et al., 2019). Social roles and positions can enhance advantages to the individual; higher ranking sows are identified as having significantly higher farrowing rates compared to low-ranking individuals (Hoy et al., 2009a). Further understanding sociality within commercial species presents unique opportunity to perceive how these roles may impact the social structure, welfare, and reproductive performance in response to social challenges and dynamic social networks.

1.5.1. Power and influence at a group level

All collective species and individuals are not equal in the social and ecological impact they have on their conspecifics, other species, or the environment. At a macro-level, keystone species (Paine, 1966, 1995) are described as having '*a disproportionately large effect on community dynamics*' (Modlmeier et al., 2014, p.53). Keystone species classify as predators, prey, plants, links, and

modifiers (Mills et al., 1993); each with the capacity to impact upon an ecological system (Table 3). While keystone species will undoubtedly impart effects on social networks and are critical for environmental and conservation purposes, a more focussed concept is required to extend upon the impact of social roles at a smaller and more localised network level.

Table 3. Empirical examples of keystone roles for each keystone category, including predators, prey, plants, links, and modifiers.

Keystone category	Keystone species	Geographical location	Removal or introduction	Effect	Authors
Predator	Fire ants (*Solenopsis geminate*)	Mexico	Removal	Increased numbers of arthropods detrimental to primary producers	Mills et al., 1993
Prey	European Rabbit (*Oryctolagus cuniculus*)	Southern Europe	Removal	Reduction of a food source for critically endangered Spanish imperial eagles (*Aquila adalberti*)	Delibes-Mateos et al., 2007
Plants	European aspen (*Populus tremula L.*)	Northern Europe	Removal	Reduction of microhabitats for multiple species including mammals, birds, Invertebrates, Fungi.	Junninen et al., 2007; Halme et al., 2013; Remm et al., 2017; Hardenbol et al., 2019;
Links	Pollinator species	Globally	Removal	Disruption to pollination networks and processes.	Martín González et al., 2010
Modifiers	North American beaver (Castor canadensis)	North America	Introduction	Dam building alters hydrology, providing wetland areas for amphibian species	Hossack et al., 2015
	Wild boar (*Sus scrofa)*	Northern Hemisphere	Introduction	Forest regeneration and landscape modification	Ramirez et al., 2018

1.5.2. Power and influence at an individual level

At a more localised level, the structure of a social network will be determined not only by the types of relationships and behaviours that influence cohesion and social connections, such as agonistic interactions or preferential associations. The structure will also be affected by individuals with increased power or influence who impact upon the fitness and survival of a group by facilitating information transference, behaviour, or disease. Often referred to as keystone individuals, these animals define as '*individuals who have a disproportionately large, irreplaceable effect on group dynamics'* (Modlmeier et al., 2014, p.53). The stability of a network can also be fundamental to the social roles of specific individuals. A study of policing behaviour in pigtailed macaques showed effective interventions of aggressive encounters were strategies only employed by the highest-ranking animals (Andersen, 2005a). Policing behaviour is pivotal for social cohesion in macaques, with increased aggression and reduced grooming and, play occurring when policers are removed from the troop (Flack et al., 2006). An expectation that the primary initiators of allogrooming would be lower-ranking animals, supports the concept of 'grooming-for-commodity' (Wubs et al., 2018), however, in some species this role is dependent on dominance rank and sex. In tufted capuchin monkeys (*Cebus apella*) it is both social standing and sex that determines initiation and receipt of grooming (Di Bitetti, 1997). Social balance is also attainable through positive interactions such as outlined in the concept of 'grooming-for-stability', a mechanism employed to maintain the equilibrium of the group, in which dominance determines the rate of initiated grooming (Šárová et al., 2016). In fission-fusion societies, as those found in pig social structure, keystone individuals can act as brokers to form links between subgroups, maintaining whole population cohesion. A study of bottlenose dolphins identified individuals, who when temporarily absent, altered the dynamics

of the community. Levels of interactions between subgroups were directly correlated to the presence of these key dolphins, increasing upon their return to the pod (Lusseau and Newman, 2004).

Despite, the plethora of keystone roles identified in wild species that impinge upon group dynamics (see Table 1. Modlmeier et al., 2014); the technique is underrepresented in the study of commercial animal interactions and social networks. The significant advantage of identifying powerful or influential individuals at a network level in a captive species is that specific individuals can be targeted and easily removed if their behaviour is detrimental to the group. It could also serve to inform intervention strategies; McCowan et al. (2018) reported that the removal of natal males from a sizeable captive group of laboratory rhesus macaque (*Macaca mulatta*) decreased aggression. A critical consideration for the application of management techniques based upon the identification of keystone individuals is the temporal consistency of social role. Powerful and influential individuals may only impart intermittent or temporary effects on social dynamics, highlighting the necessity to distinguish between 'fixed keystone individuals' and 'current occupants of keystone roles' (Modlmeier et al., 2014). A temporary occupancy can be induced by specific variables including, reproductive state, social context, and hormones (Fischhoff et al., 2007; Graham and Herberholz, 2009; Alward et al., 2019). Instability of social roles prompted by social context presents a strong argument for the importance of individuality in the behavioural response to conspecifics. Even when sociality traits are stable across contexts (Rocha et al., 2020), individuals can form judgements on the costs and benefits of altering their behaviour to adapt to inconsistencies, and personalities within group configurations (Foris et al., 2018). The stability of

social context presents a relevant avenue of investigation into the roles in commercial pigs due to dynamic systems and unpredictable social environments.

1.6. Social roles and welfare

Individuals with significant or influential social roles can affect the welfare and fitness of a group in multiple ways. The manner of how influence is implemented will depend upon the social function, imparting either positive or negative effects (Makagon et al., 2012). There are multiple terminologies to describe these keystone individuals including, key players (Croft et al., 2008), socially central individuals (Kulahci et al., 2018b), social hubs and bridges (Verdolin et al., 2014), super-spreaders (Robinson et al., 2018), tutors (Knörnschild et al., 2010), leaders (Reebs, 2000) and dominants (Ballard and Robel, 1974). Despite these definitions, within-group effects will be determined by influence upon four main processes, information transference and social learning, behavioural transmission, disease transmission, and reproduction.

1.6.1. Disease transmission

Gregarious animals are particularly at risk of disease and parasites due to their social interactions, use of shared space and resources; with a positive correlation between the density of a group and pathogen transmission rate (Sintayehu et al., 2017). Therefore, intervention and management strategies informed by identifying individuals that impact upon the rate of disease or parasite transmission is crucial to maintaining health and welfare in wild, and captive species. Transmission is bidirectional, with individuals that are socially central or more highly connected at a higher risk

of disease and with a disproportionate capacity to increase the rate of spread through a group (Zhou et al., 2006; de Freslon et al., 2019). Research has shown that 80% of all transmission rates of pathogens are contributed to by only 20% of a given population (Paull et al., 2012). Several studies into infection transmission rates have documented the impact of social roles in wild and free-roaming commercial species. Rhesus macaques that are socially central and highly connected in grooming and huddling networks impact upon the transmission rate of *Escherichia coli* through the troop (Balasubramaniam et al., 2019). Dominant and more aggressive sleepy lizards, *Tiliqua rugosa*, are less likely to avoid conspecifics in shared refuges, increasing the chance of becoming infected with ticks and engendering further spread of the parasite (Sih et al., 2018). The benefits of identifying 'super-spreaders' in animal social networks are demonstrated clearly in a recent study of endangered Hawaiian monk seals, *Neomonachus schauinslandi*, (Robinson et al., 2018). These seals are highly susceptible to protozoal infections, causing significant rates of mortality among their populations (Barbieri et al., 2016). The Robinson et al., (2018) study found that identifying highly connected seals, based upon close contact networks, improved the efficiency of vaccination programmes; proposing that only vaccinating key animals could indirectly improve the health of the entire population. The study, though, also highlighted the difficulty and time constraints that are often associated with studies of wild animals, particularly marine species in which visualisation of individuals can be challenging.

Challenges to data collection, missing data and observations would, comparatively, be significantly reduced in commercial animals, compared to wild species, a result of environmental constraint. Furthermore, the capability to identify key individuals would serve as an essential mechanism for

monitoring health and predicting disease outbreaks in commercial species, particularly as intensive farming promotes dense populations; the density of a society influences transmission rates (Pie et al., 2004). Providing support for identifying key animals within commercial species is shown in a recent study of dairy cattle (de Freslon et al., 2019). Within affiliative behavioural networks, the study identified that cows in oestrus and male calves served as keystone individuals with the potential capacity to become super-spreaders in the event of a disease outbreak. In particular, the bovines were observed engaging in significantly higher levels of interactions than their conspecifics. In reference to commercial pigs, the abolishment of sow stalls in 2013 (EU Council Directive, 2008/120/EC) has led to an increase in large, group housing systems. As most porcine pathogen transmission occurs due to nasal-nasal contact and contact with urine, and faeces (Maes et al., 2016), the opportunity for rapid disease transference throughout a commercial herd is potentially higher. Although there may be opportunities for avoidance behaviour of conspecifics, dependent on spatial allowances, essential resources will drive animals together. Despite current underrepresentation, the recent developments in the use of identifying keystone individuals as a mechanism for understanding the transmission of disease in commercial species highlight the extra benefits to the welfare and subsequent reproductive success.

1.6.2. Information transmission and social learning

There are many skills required to maintain the success of group living in gregarious species, from the etiquettes of society to the observational learning of new skills and survival strategies. While many crucial skills become acquired at a young age through vertical (parent-offspring) or horizontal information (peer-to-peer) transmission, the role of the keystone individual impacts upon any

stage of life and can extend beyond relatedness. This method of learning is described as directed social learning, in which select individuals will be acknowledged as a valuable source of information, providing a non-random and less spontaneous route of information transference (Coussi-Korbel & Fragaszy, 1995). In elephant societies, the matriarch acts as the keystone individual by representing the bank of knowledge for the herd (McComb et al., 2001). Thus, allowing for the provision of cues for social learning; the absence of a matriarch revealed an effect on responsiveness to the acoustic sound of bees, reducing herd reaction to the potential danger (King et al., 2007). The acquisition of a keystone role in social groups is not, however, restricted to those individuals traditionally perceived as dominant (Botting et al., 2018), suggesting other variables that may influence the capacity for an individual to become influential in the transmission of information and subsequent social learning. Knörnschild et al. (2010) reported that male and female greater sac-winged bat pups, *Saccopteryx bilineata*, learn complex vocalisations only through the imitation of adult harem male territorial songs. This useful skill can impact upon future reproductive success (Davidson and Wilkinson, 2004). In spined sticklebacks, *Pungitius*, it is body size that determines an individuals' capacity to become keystone demonstrators in foraging activities (Duffy et al., 2009). Individual differences in sociality can also aide social learning, imparting a detrimental effect when key animals are removed. The removal of socially central and highly connected zebrafish, *Danio rerio*, from a shoal, demonstrated a reduction in escape behaviour, necessary for survival, in non-key fish (Vital and Martins, 2013). Additionally, despite no differentiation of formal social rank, specific worker ants, *Temnothorax albipennis*, undertake informal leadership roles, dictating decision-making strategies when seeking out preferred nest sites (Stroeymeyt et al., 2011). There is additional evidence to suggest that keystone individuals are

selected for their specialised abilities, where plasticity in behaviour may serve to overcome environmental challenges or shortages in resources (Bolnick et al., 2003).

Generally, social learning and the transference of information inter- and intra-species is viewed as a positive process for improving both individual and group fitness, mitigating the costs associated with asocial learning or trial-and-error strategies. In contrast, amongst commercial species, social learning can also relate to the contagion of negative behaviours, often perceived as an indication of reduced welfare. Detrimental actions attributed to environment and transferred through social learning include, feather pecking in chickens (Nicol, 1995), weaving in horses (Ninomiya et al., 2007) and tail biting in pigs (Blackshaw, 1981). In commercial and domestic animals, social position is impactful on the effectiveness and transmission rate of social learning through imitation. Nicol and Pope (1998) found a disparity in the influence of demonstrator effectiveness in domestic hens; observers of high-ranking hens performed more accurately on operant discrimination tasks than observers of low-ranking demonstrators. Predefined leaders are also disproportionately more influential than lower-ranking individuals upon social facilitation of movement in domestic sheep and horses (Squires and Daws, 1975; McVey et al., 2018). Higher ranking individuals also have the capacity to attenuate the affective state of a social group; dominant horses were observed to reduce fear in lower-ranking conspecifics (Rørvang and Christensen, 2018). Demonstrators of behaviour have the potential to be disproportionately influential within a network, although this will only occur if the action is reinforced through imitation by the observer. The evidence shows that crucial individuals possess the ability to act effectively as demonstrators or tutors, enhancing imitations of potentially undesirable behaviours. Identifying key animals is vital for intervention or

potential removal in the event of an outbreak of negative activities, a mechanism to control the close contact.

Furthermore, key animals, of whom conspecifics are more likely to imitate, have an inordinate impact upon social learning, presenting an opportunity to approach welfare issues from a new perspective. Through identifying key animals, conditioning of positive affective states, desirable behaviours, and skills, could be utilised to enable these individuals to act as indirect conduits of transmission to the whole group. For example, a key demonstrator trained in the use of an electronic sow feeder may be particularly beneficial to inexperienced sows in group housing systems. Emotional contagion in pigs is high (Reimert et al., 2017), presenting further opportunity to implement strategies that increase positive affective state in groups premixed before reintroduction to the herd in dynamic systems. Premixing sows facilitates subgroup formation after mixing (Durrell et al., 2003), with effective diffusion of learning attributed to smaller group sizes (Ashton et al., 2019). The identification of key individuals within large intensive sow groups does present a challenge, where the formation of linear hierarchies is difficult to achieve, presenting an argument for accurate methods that allow for the identification of potential subgroups within large herds. Smaller subgroups are representative of the group sizes in wild boar, allowing for the linear hierarchies to be established and the identification of potentially crucial animals. The extent of individual differences and the multitude of keystone roles indicates the complexities involved in social learning. The benefits accrued at an individual and group level from the presence of a keystone animal in information transference and social learning networks would be advantageous in the development of alternative management strategies. As such, identification of keystone

animals in the context of learning provides a unique opportunity for exploring welfare and health in a commercial setting.

1.6.3. Behavioural transmission

While the terms used to describe keystone individuals can be interchangeable, they may relate to different processes in a social network. Information transference and social learning are dependent on the perceptions of keystone individuals by their conspecifics. In contrast, a behavioural transmission is reliant on an individual's reach and subsequent influence through a network. For example, a pig identified as being overly aggressive may not necessarily impact significantly on the diffusion of aggression through a network if they only attack the same few individuals. Moreover, influence in one behavioural network does not automatically transfer into another. Foris et al. (2019) found that dairy cows that were significant in the transmission of aggression were not also significant in affiliative behaviour interactions, with a moderate to strong stability of behaviour over the six-month study. However, the stability of behaviours could be interpreted as predictable as the cows in the study were already familiar to each other prior to the implementation of subgroups. This work demonstrates that caution must be applied when considering which animals have influence, enabling extension beyond traditional thinking, to evaluate the variables that may account for behavioural flexibility in different social contexts. This perspective requires an alternate approach, based upon social connectivity or the capacity to broker (acting as a bridge between two unconnected individuals to allow the transfer of a behaviour).

Identifying influential individuals with increased sociality in behavioural networks allows for further understanding of how behavioural patterns might emerge (Makagon et al., 2012), informing intervention and management strategies. The removal of highly social individuals from affiliative networks can be detrimental to group cohesion (Manno, 2008; Kanngiesser et al., 2011). By comparison, the removal of highly connected individuals within aggression networks may prove more beneficial to group stability (Alberts et al., 1992). Removing connected animals is particularly relevant to the spread of undesirable behaviours within commercial animals, where agonistic interactions are frequently observed (McGlone, 1985), presenting a substantial threat to welfare within sow group-housed systems. Conversely, aggressive behaviour is not a stable trait, influenced by context and social dynamics as documented in a wide range of species including, Atlantic salmon, *salmo salar* (Jones et al., 2012), cichlid fish, *Hypsophrys nicaraguensis* (Lehtonen and Wong, 2017), damp-wood termites, *Hodotermopsis sjostedti* (Ishikawa and Miura, 2012), chimpanzees, *Pan troglodytes* (Duncan et al., 2013), common fruit flies, *Drosophila melanogaster* (Nandy et al., 2016) and chacma baboons, *Papio ursinus* (Baniel et al., 2018). Although in resident-intruder tests, research demonstrates stability in pig behaviour over time that is independent of sex, age, and body weight, reflecting a consistency of aggression determined by a more complex variable such as personality (Erhard and Mendl, 1997; D'Eath, 2002). An enhanced understanding of the stability of behavioural traits over time and situation in breeding sows is, therefore, essential for the success of potential management strategies founded upon the identification of influential and highly connected individuals.

1.7. Social roles and reproductive performance

Keystone animals can impact upon reproductive performance and offspring survival. The exact nature of the influential social role will determine the direct and indirect processes that affect reproduction. Dominants have a significant, direct impact on reproduction at a group level. If these key individuals are removed from a population, whole-group mating success can be negatively affected, as demonstrated in dominant male greater-prairie chickens, *Tympanuchus cupido*. Dominant males are significantly influential in the reproductive success of a social group, as lower-ranking males are not permitted to engage in lekking; the removal of these leading individuals substantially reduces the numbers of successful mating attempts (Ballard and Robel, 1974). Keystone animals defined as leaders can indirectly influence group reproductive success as they are often attributed with the responsibility of acquiring new feeding sites, successful collective behaviour, and group movement (Dyer et al., 2009; Harcourt et al., 2009; Pruitt and Keiser, 2014). Furthermore, super-spreaders may affect reproduction and offspring survival, if responsible for the rapid transmission of disease through a social group.

The benefits attributed to keystone individuals for whole-group reproductive success are extensive but being influential or powerful does not come without cost. While there are advantages to an elevated social position (Höjesjö et al., 2002), social roles acquired and maintained through aggressive behaviour can have detrimental effects on the keystone animal (Creel et al., 2012). It may be expected that in despotic societies, low ranking individuals would be at risk of increased stress (i.e., Shively, 1998; Young et al., 2006), which is positively associated with reduced

reproductive performance. Past research though has also documented a reverse effect, with dominants at increased risk of damaging stress over a variety of species (Creel et al., 1996; Sands and Creel, 2004; Mileva et al., 2010; Silva et al., 2018). One possible explanation for the inconsistencies across taxa refers to social stability, demonstrated in a pivotal study by Sapolsky (1992). During periods of social stability, the differences between cortisol concentrations in dominant and subordinate baboons are insignificant. Sapolsky (1992) did report that during social instability in a troop of wild male olive baboons (*Papio Anubis*), a result of challenges between those close in rank, a more significant disparity in the cortisol concentrations occurred between dominants and subordinates. The relationship between stress, social stability and social role is also recently seen in commercial poultry. Carvalho et al. (2018) revealed that during periods of social stability, subordinate laying hens had higher glucocorticoid levels than dominants, with a reversal of the findings during social instability. These notable findings provide a new perspective relative to the effects of social unrest on the reproductive success of influential or powerful individuals in breeding sow herds.

Unlike their wild counterparts, commercial sows are subject to dynamic social environments, with the perpetual need to establish and maintain a hierarchy. It is recognised that in populous groupings, linear hierarchies are impossible to achieve, although the potential to fragment into smaller subgroups may be possible. Social instability influences the levels of stress-induced by a particular social role or position, as previously demonstrated. As such, it is feasible to hypothesise that even in the absence of clearly defined leaders in commercial pig herds, the reproductive performance of influential or powerful individuals may become detrimentally affected or at least

be significantly different to generic conspecifics. The relationship between stress, reproductive performance, social stability and social status or role is complicated, mainly due to contradictions within the research. For example, in the context of winners and losers, Hoy et al. (2009b) identified that low-ranking losers had significantly lower farrowing rates than high ranking winners. It must be expected that the differences in fertility rates between winners and losers are influenced by the impact of stress upon the endocrine system because cortisol levels are observed to be higher in losers than winners (Mendl et al., 1992). Although conflicting results discovered in further research show no differences in the stress responses between winners and losers (Camerlink et al., 2016b). Also, a study of disease susceptibility found subordinate sows were more at risk of mortality and morbidity than dominants in response to a virus challenge, albeit conducted under stable social conditions (Hessing et al., 1993). These inconsistencies reflect that there remains a lack of consensus on the relationship between social role or position and reproduction in breeding sows.

1.8. Social Network Analysis

Exploring the complicated relationship between social structure, behaviour, reproduction, and social roles in animals is a crucial avenue of investigation for enhancing welfare, both in wild and captive species. The capacity to understand the influence of a few key individuals on the social structure at the group level requires a methodology capable of transitioning from a macro to a micro level of observation. A strategy that has previously presented a challenge in the study of animal behaviour (Lima and Zollner, 1996). In recent years there has been an upward trend in the application of social network analysis (SNA) in the field of animal science, highlighting the

technique as a valuable research tool (Koene and Ipema, 2014; Davis et al., 2018). Social network analysis is described as a strategy that can '*improve our ability to scale up from the individual to the population by establishing why certain patterns of association develop and how inter-individual association patterns affect population-level structure*' (Croft et al., 2008, p1).

1.8.1. Construction of a network: Extending beyond the dyad

Social network theory is grounded in the analysis of the relationships or social ties that occur within any given network. Identification of individuals is, therefore, fundamental to the construction of a network and evaluation of how individuals might impart influence within a social group. Individuals are designated as nodes and the social ties between them, reflective of any behaviour, are defined as edges (Croft et al., 2008). Edges are represented as lines between nodes. The edges can be weighted in which the total frequency of interactions or strength of ties can be observed or unweighted. Croft et al., 2011 refers to the collection of weighted ties as the 'gold standard' of social network matrices; as binary measures do not fully represent the strength of ties between individuals (Lusseau et al., 2008). Edges can be directed or undirected, with directed ties demonstrating the initiator and recipient of an interaction (Wey et al., 2008). Bidirectional ties indicate if the behaviour is reciprocated between the initiator and receiver. The direction of interaction is indicated with an arrow at the end of an edge (Borgatti et al., 2018). Such information allows for the construction of a visual graph called a sociogram (Wey et al., 2008), that is interpreted at an individual, dyadic, or at a group level (Figure 1). Nodes can be assigned attributes (i.e., sex, parity) to allow for further analysis, such as homophily effects on associations.

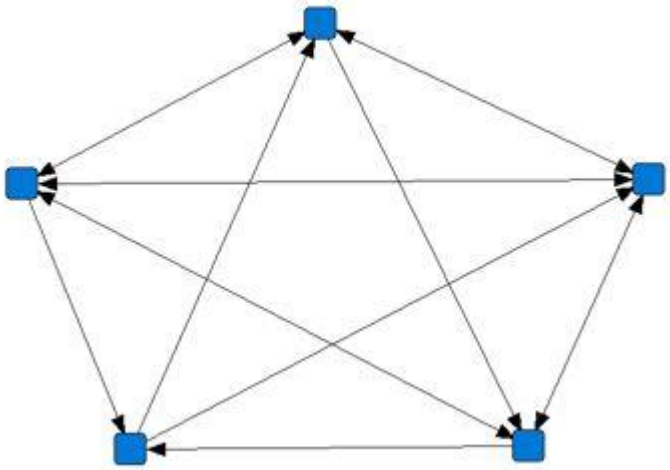

Figure 1. Simple five-node illustration of a sociogram with unweighted ties and directed interactions between nodes, as indicated by arrowheads. Reciprocation of social ties is not occurring within every interaction.

A key benefit of social network analysis is the ability to extend beyond dyadic interactions; nodes may have both direct and indirect effects and beyond sociograms, SNA provides quantitative metrics of network position. Direct ties are the immediate level of interactions within a dyadic encounter; the number of direct interactions a node engages in is calculated to present a total count referred to as the degree centrality. In a directed network, degree centrality is additionally defined as indegree centrality, the total number of received ties and the outdegree centrality, the total number of initiated ties (Borgatti et al., 2018). Degree centrality is pivotal for identifying the sociality of any individual and thus, their social positioning and potential effect upon a network. A recent study of the exploratory behaviour of wild house finches (*Haemorhous mexicanus*) found weighted degree centrality was a predictor of latency to explore; individuals with high degree centrality in a foraging network reacted more quickly during a novel environment task (Moyers et al., 2018). Also, low degree centrality, reflective of reduced sociality, can alter expected behaviour. For example, it is generally believed that group living increases a sense of security (Creel et al.,

2014). Conversely, the emergence of SNA in animal behaviour research has revealed that it is also sociality that influences how safe an individual might perceive themselves to be. Low degree centrality alters the alarm call structure of yellow-bellied marmots (*Marmota flaviventer*); socially isolated individuals engage in significantly louder alarm responses than their socially central conspecifics (Fuong and Blumstein, 2019). Indicating that existing on the periphery of a social network may have detrimental effects on the wellbeing and fitness of an individual.

Individuals can also impact positively or negatively on a social group through their indirect interactions, connecting with partners of their chosen social tie (Croft et al., 2008). In a network, specific individuals have the potential to transfer a behaviour (or information and disease) between two previously unconnected nodes. In SNA, one metric that enables transmission is betweenness centrality, defined as the total number of shortest paths that flow through an individual linking two previously unconnected nodes to each other (Brent, 2015) (Figure 2). Individuals that sit upon multiple shortest paths have increased transference potential, highlighting betweenness centrality as a valuable metric in the investigation of individual behaviour on welfare and reproductive performance at a group level. Nodes with high betweenness centrality have the potential to spread disease or detrimental behaviours more rapidly within a social group or between two previously unconnected social groups (Weber et al., 2013). Conversely, these influential nodes contribute positively by increasing the spread of fitness-enhancing behaviours, information or maintaining social cohesion (Lusseau and Newman, 2004; Brent et al., 2013; Verdolin et al., 2014). It must be noted that degree centrality and betweenness centrality should be carefully discriminated between as the two metrics do not necessarily correlate.

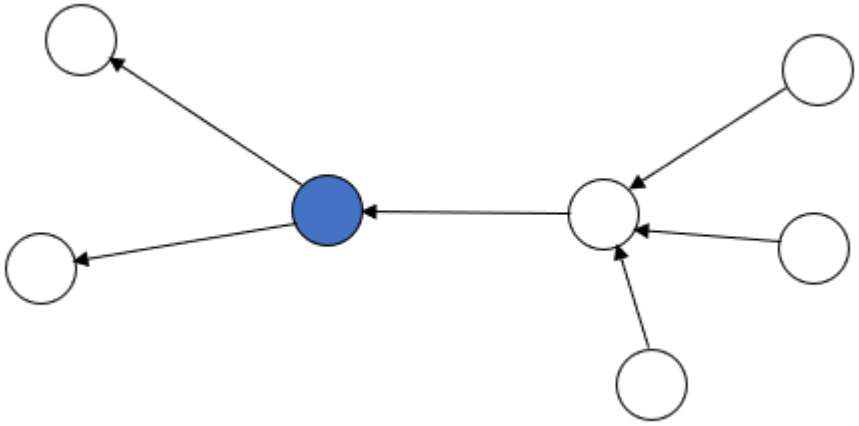

Figure 2. Illustration of an influential individual (blue node) in a social network that acts as a bridge to connect previously unconnected individuals (white nodes) through the transmission of behaviour, pathogens, parasites, or information transference.

1.8.2. The application of social network analysis and welfare

The ability to explore the impact of social structure and dynamics at an individual level provides an enhanced understanding of sociality. It should not be assumed that environmental or social challenges will affect every animal equally, and the concept of keystone individuals includes evidence to support the inequality of effects an influential animal can impose upon a group. The application of SNA enables the identification of important and influential individuals because it allows for the construction of a network and is based upon all complex behavioural interactions within a range of agonistic, affiliative, communication, transference, or movement systems (Ortiz-Pelaez et al., 2006; Abeyesinghe et al., 2013; Büttner et al., 2015; Potvin et al., 2019). With a focus on identifying the effects of individual behaviour at a group level, SNA allows for the evaluation of bidirectional interactions, highlighting the initiators and recipients (Borgatti et al., 2018). A necessary process when considering welfare issues and subsequent management strategies involving commercial pigs because enhanced social connections increase opportunities to impact

positively or negatively on a social group or individual (Balasubramaniam et al., 2019; Sabol et al., 2020). The ability to identify significant initiators or receivers of aggression in intensive herds could serve to inform management strategies. By comparison, reduced social connections can alter individual responses that also affects group fitness and survival (Fuong and Blumstein, 2019). Suggesting a scale of behaviour in which the frequency of interactions can be used to evaluate temporal changes in individual and group behaviour that might arise from social or environmental challenges. Examples of this are the social roles and behaviour of Atlantic salmon (*Salmo salar*), which alter in response to unpredictable feeding schedules (Jones et al., 2010) and submission plasticity in cichlid fish (*Neolamprologus pulcher*), influenced by a reduction in shelter availability (Reddon et al., 2019),

A proposal was put forward to show that animals may become highly connected in a network due to a unique or enhanced skill that is desirable and beneficial to conspecifics. Kulahci and Quinn (2019) proposed the concept of 'valuable social partners' in which disproportionate social connections were directed at specific individuals. SNA studies have revealed that highly connected individuals have enhanced ability over their conspecifics to learn about their environments. Recently, an association has been documented between social centrality and learning, in which individuals become highly connected, and acquire new information following novel foraging tasks in free-ranging ring-tailed lemurs (*Lemur catta*) (Kulahci et al., 2018b). In male killer whale pods (*Orcinus orca*), an association was also made between social position and survival rates (Ellis et al., 2017). The three-year study proposed that highly connected males became socially 'desirable' due to their enhanced ability to seek out resources and subsequent food sharing during times of low

salmon abundance. In comparison, in great tits (*Parus major*), individuals identified with fewer exploratory behaviours were significantly less socially connected than birds with considerable exploratory skills (Snijders et al., 2014). The application of the concept of 'valuable social partners' could feasibly be applied to any behaviour that may be considered fitness-enhancing, forming the basis of one possible explanation for the development of preferential associations. A bond yet to be agreed upon in commercial pigs, with random and non-random associations difficult to discriminate between using traditional methods (i.e., Durrell et al., 2004).

Despite these advantages, the method remains underrepresented in animal network studies (Hobson et al., 2013; Croft et al., 2016). The lack of representation extends even further when considering commercial species, with very few studies using the SNA approach to investigate the relationship between social structure, social role, and welfare in intensive farming systems. These limited studies have included dairy cattle in which SNA has identified that sociality is not equal and behavioural responses to the social environment are context dependent. SNA has also shown that remixing in cows promotes inconsistency in social structure despite high centralisation and reveals that subgroups do not develop in cattle herds. The method further demonstrates that preferential associations can occur between conspecifics with selective temporal relationships influenced by individual attributes such as age, breed, gregariousness, milk production and lactation (Boyland et al., 2016; Foris et al., 2019; de Freson et al., 2019; Rocha et al., 2020). In laying hens, SNA has been applied to investigate preferential associations, although it remains to be established if birds engage in discriminatory social selections of conspecifics (Abeyesinghe et al., 2013). Finally, limited SNA studies of pigs have identified that following a mixing event, the social metric of density is a

good indicator of overall group aggression. Research also demonstrates that weaned pigs are more aggressive after remixing compared to finishers or gilts, indicating a relationship between behaviour and age. SNA has revealed that grouping pigs according to their social preferences increases positive sociality; reducing tail-biting and the network properties including density, degree centrality, the clustering coefficient and centralisation, commonly detected after 24h post mixing. Thus, presenting as a good predictor for chronic level aggression in a group (Büttner et al., 2015; Foister et al., 2018; Li et al., 2018). Recent pig literature has also highlighted the value of SNA in the prediction of aggressive behaviours at an individual level and the impact of context-dependency on behavioural stability (Agha et al., 2020; Turner et al., 2020). The application of SNA to the study of commercial animal welfare has provided valuable insight into the limited literature, demonstrating the potential for its application in the study of behavioural stability and social structure of gestating sows in dynamic systems.

1.9. Conclusions

There is an increasing body of evidence to support the value of identifying social roles using social network analysis in the context of welfare and reproductive performance. Although this avenue of research is still in its relative infancy, very few studies have committed to the research of social roles and social structure in commercial animals, particularly regarding positive behaviours. The application of SNA will enhance understanding of the social processes employed in dynamic herds. As aggression in networks of gestating sows continues to present as significant welfare and economic concern; this research will provide new insights into the development of management and potential intervention strategies through a novel approach.

Chapter two:

General methods

2. General Methods

2.1. Animals and housing

The study was carried out at Sturgeons farm, Writtle University College, Chelmsford, Essex (United Kingdom) between the 20th November 2017 and 21st January 2018. The pig unit can support a herd of up to 80 sows; the study group consisted of a commercial cross of Large White-Landrace and Pietrain breeds; parities of one to seven. Sturgeon's farm operates a dynamic production system in which small groups (maximum of 12 individuals) are removed or mixed into the herd during each three-week production cycle (PC1 = Production cycle 1, PC2 = Production cycle 2, PC3 = Production cycle 3). The repeated period of production follows the pattern, farrowing week, breeding week, and weaning week. Individuals may additionally exit the herd due to severe illness or culling. The numbers of observed sows fluctuated in response to the dynamic system, with a minimum rate of 56 sows in the dry barn when the farrowing house was operating at full capacity.

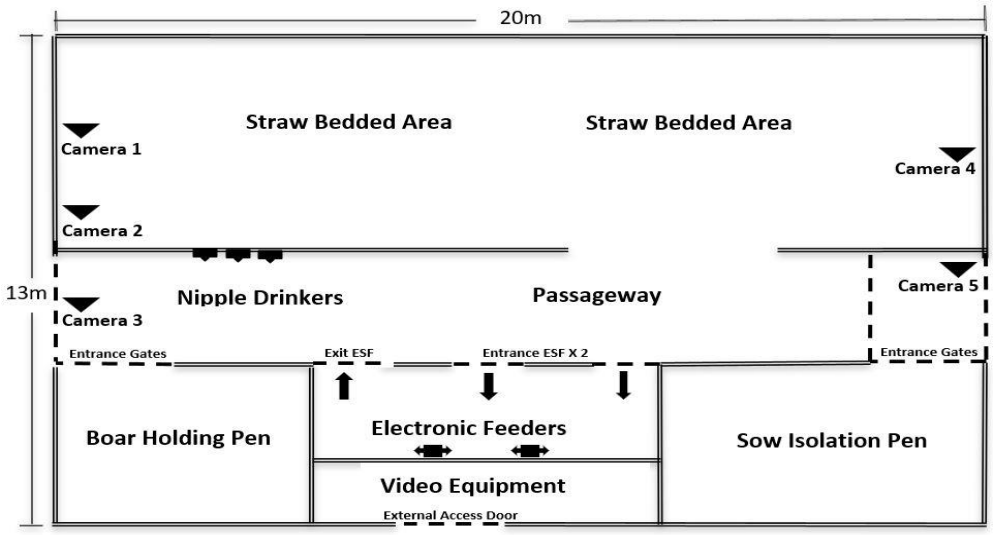

Figure 3. Schematic of the dry sow barn at Sturgeons farm, Writtle University College, Chelmsford, Essex, UK, indicating the main functional areas, dimensions of the barn and position of cameras. Key functional areas include the straw bedded area, the electronic sow feeding area, the nipple-drinkers, and the passageway.

During gestation, sows remained in the dry barn with free movement to all functional areas and conspecifics, and *ad libitum* access to straw. Functional areas included the straw bedded resting area, the passageway, the drinking station, and the electronic sow feeding (ESF) station (Figure 3). The straw bedded area measures 20m x 6.5m, with additional space in the passageway of 17m x 3m. Two ESF and five nipple drinkers are located along the shared passageway. The ESF resets at 15:00 h. The sows were apportioned rations of Delta Renovo TD dry sow pellets (a complete feed for breeding sows) with individual quotas metered electronically and determined by body size. Straw in the bedded area is refreshed every Monday, Wednesday, and Friday. The passageway gets routinely cleared once a week with a complete clearance of the straw bedded area occurring every six months. For individual identification, each sow was marked with coloured dots, stripes or both on their backs using a stock-marker. The coded markings corresponded to an individually allocated ear tag number allowing for cross-referencing of farm information held for each sow. Refreshment of the markings was required every 1-2 weeks. The individual marking and coding approach are consistent with related research (i.e., Durrell et al., 2004; Büttner et al., 2015).

2.2. Data collection

2.2.1. Sow health, farrowing and reproduction data

The farm diaries and liaison with the pig unit manager provided relevant information pertaining to parity, farrowing date, culling, permanent removal from the herd, insemination date and date of remixing. Information relating to reproductive performance was also recorded in the farm diaries including, live-born piglets, stillborn piglets, mummified foetuses, low viability, scours, lameness, hypothermia, crushing and any other cause of piglet mortality following birth until weaning. Access

to all ESF computer data files was made freely available on the farm computer system; the data included date and time individuals accessed the feeders.

2.2.2. Video observation data

A total of five CCTV H.265 4Mega Pixel Eyeball PoE, infrared Dome cameras were installed in the dry barn to capture and observe sow behaviour. Each camera was positioned to provide unobstructed, direct visual access to all essential functional areas. The areas included the straw bedded area, the passageway, the isolation pen, the ESF area and the drinkers (Figure 3). The recording of footage continued non-stop throughout each production cycle utilising two H.265 8 Channel Network Digital Video Recorders (DVRs) fitted with 3TB hard drives. The operational DVR was housed in another part of the barn, accessible without disturbing the sows and connected to a 21.5" LED Hi-Res VGA, DVI, HDMI monitor. At two-week intervals, the DVRs were rotated, then connected to a workstation computer with video software that allowed for close observation of the captured footage. The specialist software allowed for close analysis of all behaviours using a timed playback system; with the option to slow down or speed up footage and zoom in. The equipment was supplied and installed by Communicate UK, Chelmsford, Essex. Video camera use reduced disruption to the animals, eliminating effects upon behaviour due to the researcher's presence. The implementation of cameras is consistent with other social network studies (Büttner et al., 2015; Greenwood et al., 2017).

Following Study 1, (conducted before the social network study), three hours per day were selected for observation, proven to be the optimum periods when the sows were most active. The study

revealed that the most effective times for data capture were in the morning (08:00-09:00), the afternoon (15:00-16:00) and the evening (20:00-21:00). The hours between 23:00 and 06:00 remained excluded from the study due to a proposed reduction in activity (Stuckenborg et al., 2011) and the fact that the artificial lighting in the barn turned off at 23:00. Observations for production cycle 1 (PC1) occurred 20th November to 10th December 2017, production cycle 2 (PC2) occurred 11th December 2017 to 31st December 2017 and production cycle 3 (PC3) occurred 1st January 2018 to 21st January 2018. The video observations occurred on seven preselected days of each production cycle, including the day before remixing (day 20) and the day of mixing (day 21). The observations continued for the three consecutive days following a mixing event (days 1, 2, 3), consistent with previous research (i.e., Büttner et al., 2015) and following the time when the herd re-stabilises its social structure (Hemsworth et al., 2013). Days 7 and 14, following remixing, were also selected to allow for temporal changes in behaviour. The same researcher carried out the behavioural observations. The next section provides a brief overview of study 1.

2.2.3. Study 1: Investigation of sow activity

2.2.3.1. Main aims

- To establish the most effective timings for data collection of the behaviours in the social network study.
- To test the feasibility of capturing agonistic behaviours.
- To test the use of the cameras and their positioning within the dry barn.

2.2.3.2. Animals and housing

Study 1 was conducted at Sturgeons farm, Writtle University College, Essex over three weeks in August 2017. The study group consisted of 60 commercial crosses of Large White-Landrace and Pietrain breeds, housed in a dry sow barn (Figure 3).

2.2.3.3. Data collection

The study selected two days per week for observations including one day when new straw was provided and one day when mucking out did not occur, allowing for comparisons between those days. An all-occurrences sampling method was applied to agonistic behaviours between the hours of 07:00 and 23:00 on the preselected observation days. The hours between 23:00 and 06:00 were excluded due to a proposed reduction in behaviour during that time (Stuckenborg et al., 2011) and the strip lighting in the barn was turned off between those hours. The frequency, locality and intensity of agonistic behaviours were recorded. Sow activity was recorded using five CCTV H.265 4Mega Pixel Eyeball PoE, infrared Dome cameras positioned to capture interactions in the key functional areas including the straw bedded area, the passageway, the feeding area, and the drinking area. Animals were not marked for individual identification; it was not required for this stage of the thesis. In total, 96 hours of agonistic behaviours were taken forward for analysis. The same researcher carried out the behavioural observations.

2.2.3.4. Data analysis

All tests were conducted in SPSS version 22.0 (Armonk, 2013, NY: IBM Corp) with an alpha level of 0.05 applied to all statistical analyses. Repeated measures ANOVAs were used to test for differences in the levels of aggression between days and hours of observation. Post hoc testing

applied a Bonferroni correction to identify in which hours there were significant differences in agonistic behaviours.

2.2.3.5. Results

There were no statistically significant differences in the levels of agonistic behaviours between days (F (2.6, 38.5) =1.35, p = 0.27), suggesting that the provision of new straw did not increase aggression throughout the day. Although, aggression increased in the hour proceeding the introduction of new substrate. No differences in behaviour were also found between weeks, F (2,30) =2.10, p = 0.14. In contrast, significant differences were revealed between hours of observation (F (2.5, 12.4) =7.42, p < 0.01). During the morning (07:00 -12:00), the highest mean frequency of aggression occurred between 08:00-09:00 (46.5 ± 9.24). During the afternoon (12:00 - 17:00), the most aggression occurred between 15:00-16:00 (45.0 ± 6.04). These times are consistent with activation of the ESF. During the whole day, the highest mean frequency of behaviour occurred during the evening (17:00 -23:00), with the greatest aggression seen between 20:00-21:00 (62.2 ± 7.07).

2.2.3.6. Discussion and recommendations

Aim 1: To establish the most effective timings for data collection of the behaviours in the social network study.

The results demonstrated the most effective times for data collection in the social network study, times when the sows were most active. Recommendations for data collection times are between

08:00 -09:00, 15:00-16:00 and 20:00-21:00. Times are based upon descriptive statistics and a view to equally distribute observation periods throughout the day.

Aim 2: To test the feasibility of capturing agonistic behaviours.

No issues occurred when identifying agonistic behaviours; however, following observations of chasing, this behaviour will be included in the social network study.

Aim 3: To test the use of the cameras and their positioning within the dry barn.

No problems were encountered with the positioning or function of the cameras. Every corner of the barn was visible, and video footage captured was of high clarity. Changing of the DVR box every two weeks ran smoothly.

2.3. Network construction

2.3.1. Visualisation of the networks

Graphical visualisations of the behavioural networks in each production cycle were constructed in Ucinet 6 (Borgatti et al., 2002) using NetDraw through the creation of sociograms. The sociograms were created using spring embedding. Spring embedding refers to the graphical layout algorithm which determines the layout of a sociogram through optimising the visual aesthetics of the graph. This optimisation is created to ensure correspondence between point and path distance between nodes. Further ensuring that nodes are not too closely positioned together and implementing the appearance of equal length lines (Borgatti et al., 2018). Individual sows are depicted as nodes, represented as 2D squares. The sociograms illustrate directed ties, in which the initiator and recipient of behaviour are shown; allowing for the visualisation of who approached whom. The

direction of the tie is indicated with an arrowhead. Attributes including subgroup and social position have been added to some sociograms and depicted by a colour-coded key.

2.3.2. Identification of subgroups

Subgroups were determined by the connectedness of an individual to conspecifics, quantified by the application of *k*-cores to each behaviour network across the three production cycles. A *k*-core is a subgraph in which every individual has a degree *k* or more connections with conspecifics within the subgraph (Borgatti et al., 2018). For example, in a 3-core subgraph, nodes will be connected to at least three other nodes, which in turn are connected to at least three or more other nodes. The *k*-core value denotes the minimum number of individuals a sow connects but does not show the weight of interactions (Figure 4).

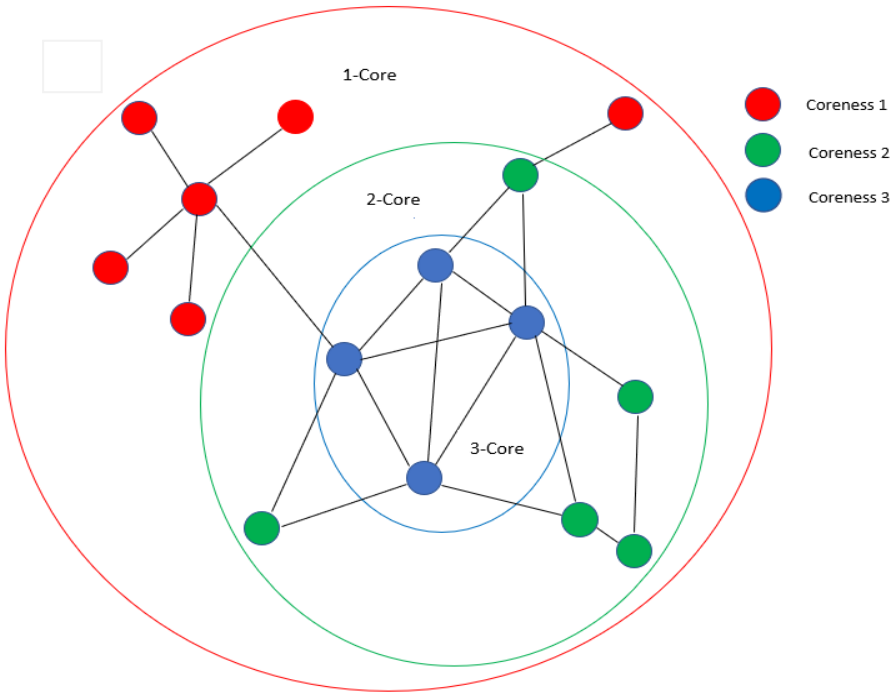

Figure 4. Illustration of *k*-core composition in a network. Nodes are assigned a coreness value determined by the minimal number of connections to other nodes. Nodes can be connected to other nodes in a different k-core subgroup. For example, in the figure K1 nodes can be connected to either K2 or K3 nodes.

The application of *k*-cores to a given network provides a number of functions, it provides an overview of cohesion, allows for subgrouping and the action of pruning nodes. Pruning nodes is a strategy to reduce the number of nodes within a network by eliminating nodes from the periphery of the social group (nodes with the lowest coreness value) and continuing to eliminate nodes until the central core (nodes with the highest coreness value) remains (Borgatti et al., 2018). Coreness values refer to the degree *k* connections that a node has with other nodes in the network. Unlike the traditional measures of subgrouping that include cliques or the clustering coefficient, *k*-cores are more relaxed and do not require significant cohesiveness within the cores (Borgatti et al., 2018). *K*-cores are also more flexible in the inclusion of nodes, thereby eliminating immersion in only one subgroup by enabling individuals to join a *k*-core even if they are connected to other *k*-cores and disregards how many nodes an individual may not be connected to (i.e., K1 sow may have a connection to a K4 sow). In this study, *k*-cores were applied as the formation of subgroups may develop in large groups when no clear social hierarchy can be achieved (Gonyou, 2001) and the strength of bonds (clustering coefficient) were weak. The application of these subgroups allows for an investigation of prominence and influence at a level representative of individual sociality, rather than whole group behavioural patterns. A sow could potentially have low connectedness within the herd but may still have a disproportionately higher connectedness than conspecifics of the same *k*-core.

2.4. Social network properties at a group level

Descriptions of social network terminologies are additionally outlined in the Glossary (Page 266).

2.4.1. Density

Density refers to the proportion of all possible dyadic ties that are present within a social network. In this study, it relates to the proportion of agonistic interactions or preferential associations. Low density indicates there is little cohesion or connectedness between all herd members. For example, a density of 0.15 represents that only 15% of all potential ties are present within the population.

2.4.2. Reciprocity

Directed networks have four potential dyadic relationships that can occur; A does not have a relationship with B (null dyad), A interacts with B (asymmetric dyad), B interacts with A (asymmetric dyad), or A and B interact with each other (symmetric dyad). Reciprocity can be inferred from density; low-density networks contain higher levels of asymmetric dyads and null dyads; shown to be more unstable and less cohesive. In contrast, high-density networks are more stable (Zemljic and Hlebec, 2005). The maximum value for reciprocity is 1 (perfect reciprocity), consisting of only symmetric dyads. The minimum value is 0 (anti-reciprocity), consisting of only asymmetric or null dyads. To ascertain if reciprocity is occurring by chance, the reciprocity index can be compared to the expected reciprocity level (i.e., density). The higher the index is from the expected value, the more likely that reciprocity is not random. In this study, the arc reciprocity method has been applied. Arc reciprocity counts the number of arcs (directed edges) and calculates the proportion of arcs that are reciprocated. The method includes the number of reciprocated arcs divided by the total number of arcs (Borgatti et al., 2018).

2.4.3. Clustering coefficient

The clustering coefficient reports on whether there is transitivity or 'clumpiness' occurring in a network and is based upon the concept that friends of friends will also become friends (triadic closure) (Brent, 2015). The coefficient evaluates that if A and B are connected, and B and C are connected, to what extent will A and C have interactions. Low transitivity demonstrates the ties between individuals are weak, with no triadic closure. By contrast, high transitivity shows that the relationships are strong, with triadic closure. Results are reported on a scale between 0-1, with 1 representing perfect triadic closure and 0 representing no triadic closure. Two measures of clustering can be evaluated, the overall graph clustering coefficient and the weighted overall graph clustering coefficient. Borgatti et al. (2018) suggest that the use of the weighted overall graph clustering coefficient is the most effective method for measuring clumpiness, and this method was selected for this study. The clustering coefficient is compared to density to evaluate the extent of clumpiness; the further the coefficient is from density the clumpier the network structure will be.

2.4.4. Centralisation

Centralisation is a group-level social network metric applied to each production cycle for both the preferential association and aggression networks to determine the extent to which each network was dominated by specified individuals (Borgatti et al., 2018). The range of centralisation is determined by the variance and equality of individual centrality in a social group (Wasserman and Faust, 1994). Inequality of centrality metrics will provide a centralisation value closer to one and indicate individuals within the group with a disproportionately higher level of centrality than their

conspecifics. Decentralised networks will reflect greater equality between individual centrality metrics and a centralisation value closer to zero.

2.4.5. E-I Index

The E-I Index is a measure of group embedding and evaluates the extent in which homophily or heterophily based upon ego-similarity is occurring within a network (Borgatti et al., 2018). The E-I Index reports on a scale from -1 (perfect homophily) to 1 (perfect heterophily). In this study, the E-I Index was applied to production cycle 1 to identify the extent to which sows were assorting by parity, familiarity (based upon remixing group) and sociality (based upon coreness value), identifying the development of potential subgroups within the herd. Parities ranged from one to seven, breeding groups (1-7) were organised based upon farrowing data and coreness values (*k*-cores) ranged from one to four.

2.5. Social network properties at an individual level

2.5.1. Degree centrality

Degree centrality is an individual-level social network metric and refers to the total number of behavioural interactions that an individual has within a network (Borgatti et al., 2018). Degree centrality is a measure of prominence within groups and subgroups (Gero et al., 2013). In this study, the preferential association and aggression networks distinguish between received ties (indegree) and initiated ties (outdegree), allowing for the construction of directed sociograms. In the preferential association networks, degree centrality (combined indegree and outdegree) for

each sow was taken forward for analysis. In the aggression networks, only outdegree centrality for each sow was taken forward for analysis to investigate the effects of being aggressive.

2.5.2. Betweenness centrality

Betweenness centrality is an individual-level social network metric that is a measure of the total number of times an individual falls along the shortest path between two previously unconnected individuals (Borgatti et al., 2018). Betweenness centrality is a measure of influence (Borgatti et al., 2005; Opsahl et al., 2010) as it indicates who are the individuals with the capacity to control the rate and flow of behaviours (Büttner et al., 2015), information (Brent, 2015) and disease (Naug, 2008) through a network by distinguishing between individual betweenness variance (Croft et al., 2008).

2.6. Quantifying missing data

Due to the dynamic nature of the herd in the study, all sows were not permanently or consistently present during the 63 h of video recordings observed. The data were weighted to account for the hours that individuals were missing from the study. The coefficient applied to both degree centrality, and betweenness centrality for absent sows is, $y = n/x$.

Where:

y = weighted value of interactions per hour observed

n = value of either degree centrality or betweenness centrality

x = number of hours observed

2.7. Quantifying the proportion of time sows were socially prominent or influential

To establish the proportion of time that sows were quantified socially prominent or influential relative to how many times they were observed in any given production cycle, the following description is provided:

33% = Sow is in three production cycles and only quantified once.

67% = Sow is in three production cycles and quantified twice.

50% = Sow is in two production cycles and only quantified once.

100% = Sow is quantified in every production cycle they were identified.

2.8. Ethics

Form AW1-Animal welfare, Writtle University College, reference: 98363980, 04/04/17

2.9. Data analysis

Social network metrics and sociogram constructions were performed in NetDraw and Ucinet 6, version 6.634 (Borgatti et al., 2002). Matrices for all agonistic and preferential association networks were prepared in Microsoft Excel and imported into Ucinet. Statistical analysis was performed using a range of R packages, version R.3.4.1. (R Development Core Team, 2017) and will be described in greater detail in each chapter.

Chapter three:

Do pigs have friends?

3.1. Introduction

Thriving community living between gregarious species is dependent on the role of sociality, enabling the formation of beneficial, complex interactions between conspecifics to engender positive evolutionary and ecological outcomes. Achieving maximum fitness outcomes at an individual level occurs due to the proximate mechanisms of sociality including information transference of resource acquisition (Harel et al., 2017), disease transmission (Stockmaier et al., 2018), problem-solving (Borrego and Gaines, 2016) and decision making (Gil and Hein, 2017). Robust threat assessments and predator avoidance positively correlate to socially bonded groups (Dostie et al., 2016). Recent research has also demonstrated that individuals in larger groups become less vigilant, suggesting an increased sense of security (Mady and Blumstein, 2017). Furthermore, socially bonded animals experience greater emotional wellbeing, perpetrating positive effects on cognitive development, physical development, health, and reproductive success (Trezza et al., 2011).

The social structure of wild boar aggregations reflects such an organisation of reciprocated cooperation and complex social dynamics (Focardi et al., 2015). As a para-social species, wild boar form small matriarchal herds; in which there is a parental investment with cohabitation between adults and offspring inside a structured hierarchy. The formation of bonds between individuals provides advantages through the direct or inclusive fitness benefits of group living, allowing for diverse behaviour and genetics (Ashton et al., 2019; Whitehead, 2020). Nevertheless, behavioural strategies and cooperation cannot be considered as stable. When individuals are subjected to

extrinsic factors, such as environmental changes, group size or composition and increased resource competition, alterations to the dynamics of a community will occur (Boumans et al., 2018); affecting the social network at an individual and group level.

Within a commercial environment degradation of the social structures that pigs are innately adapted to occurs in response to large herds, whereby, self-regulation of group size, as would be expected in a natural setting is unavailable. Additionally, unrelated animals are subjected to transient groupings and repeated hierarchical challenges, increasing the prevalence of despotic behaviour and agonistic interactions. Despite the intensity of group living under these conditions, domestication has eradicated the need for cooperative strategies in defence of predation. It has also, to some extent, reduced the direct competition between conspecifics for food acquisition, particularly in sequential feeding systems. Estevez et al. (2007) proposed that '*resource monopolisation'* and increased aggression occurs when feeding sites are positioned too closely together, resulting from an increased density of animals. Although competition for other valuable resources, such as enrichment, occurs when environments are bereft of alternative stimuli, beyond the addition of substrate which enables '*proper investigation and manipulation activities*' (European Commission, 2001/93/EC). The benefits of affiliative relationships are documented (Rault, 2012, Rault, 2019); however, research into these interactions between sows as a mechanism for coping with social and environmental challenges remains under-represented.

Differentiating between preferential social interactions, particularly as a mechanism of social support and random interactions presents intriguing challenges. In captivity, spatial constraints will

confound observations of social behaviour, due to the complexities of environmental heterogeneity. These complexities will impact upon how, why, when, and where interactions will occur. It cannot be assumed that proximity between conspecifics is exclusively motivated by the need to seek out 'a friend' or represent an affiliative relationship. Durrell et al. (2004) highlighted this in a previous study of preferential associations between pigs. The study concluded that although unrelated pigs may form affiliative relationships, results were inconsistent due to the inability to disentangle perceived preferential associations and proximity (preferred lying location). The need to separate any confounding factors is further supported by Spiegel et al. (2016), who proposed that; '*Resources may force individuals to aggregate independently of sociality'.* Therefore, careful consideration must be applied to the methodological design of sociality studies to ensure that what is being measured accurately reflects the criteria proposed by the research questions.

Social network analysis (hereafter referred to as SNA) in the field of animal science has predominantly been utilised in the study of wild animals. In recent years, however, the establishment of SNA as a useful tool for evaluating the welfare of captive animals and determining appropriate management strategies has been demonstrated (Koene and Ipema, 2014). The range of animal network studies is increasing, concerning a plethora of species, and addressing numerous research questions. Examples include identifying effective feeding schedules in Atlantic salmon (*Salmo salar*), the role of homophily and social stress in dairy cows (*Bos Taurus*), policing behaviour and group dynamics in pigtailed macaques (*Macaca nemestrina*), and the impact of social bonds on

fertility in female chacma baboons (*Papio ursinus*) (Flack et al., 2006; Jones et al., 2010; Boyland et al., 2016; Silk et al., 2018).

An established framework for the investigation of complex social behaviours (Davis et al., 2018), social network analysis allows for observations of interactions, both in terms of proximity and behaviour. This approach enables modelling of the social connections between individuals (nodes) and information on the type of behavioural interactions (edges) between nodes, where ties between nodes are represented as an array of behaviours. Additionally, the edges between nodes can have weight (the frequency or strength of interactions) and direction. Direction demonstrates which individual is the initiator of a behavioural interaction and which individual is the receiver (Wey et al., 2008). Such information allows for a modelled construction of a social network at a group, dyadic and individual level. This process also provides for temporal changes to the network to be captured with measures such as density, centralisation, ego networks, clustering coefficients, identification of components and subgroups.

The application of SNA in terms of animal management has consistently enhanced the scientific understanding of how sociality and related interactions impacts upon welfare and productivity. The approach enables the detection of changes to the stability of networks, engendering the possibility of intervention and preventative strategies that are 'tailor-made'. However, despite these advantages, few network studies have been applied to the investigation of specified behaviours and social structure in domestic pig herds. One known study by Büttner et al., (2015a) was able to infer changes to the network structure of repeatedly remixed pigs, determined by levels of

agonistic interactions, indicating the potential to impact upon the critical stage of production in which intervention would be most effective.

The current study aims to define the network characteristics of a dynamic sow herd over a three-week production cycle by applying the novel measure of SNA. Through the application of directed socially discriminatory behaviour, an investigation will be conducted into the role of preferential associations and, the formation of ties between individuals as a mechanism for providing social support. The study will also seek to identify the confounding variables, such as social differentiation (parity and familiarity) that impact upon the development of affiliative associations. By identifying how stable networks could be achieved, even within a dynamic system, the value of the findings may be used to enhance and inform current grouping practices (at a local level) to minimise agonistic behaviours that are detrimental to overall wellbeing.

3.2. Methods

Chapter two provides a detailed description of the methods. A summary is outlined in the following section.

3.2.1. Animals and housing

The study was conducted at Sturgeons Farm, Writtle University College, Chelmsford, Essex between November, and December 2017. The study group consisted of a commercial cross of Large White-Landrace and Pietrain breeds; parities one to seven, housed in a dry barn. Sows were fed on a complete feed for breeding sows through electronic sow feeders, which reset daily at

15:00 h, with additional access to straw. Sturgeons Farm operates a dynamic system in which small groups of sows are remixed into the main herd every third Tuesday. There is a repeated cycle of production following the pattern, farrowing week, breeding week, and weaning week. For individual identification, each sow was marked with coloured dots, stripes, or both on their backs. Colour codes corresponded to the ear-tag number.

3.2.2. Data collection

3.2.2.1. Sow data

The farm diaries and liaison with the pig unit manager provided information concerning parity, farrowing date, date of remixing and remixing group.

3.2.2.2. Video observation data

A total of five CCTV H.265 4Mega Pixel Eyeball PoE, infrared Dome cameras were installed in the dry barn to capture and observe sow behaviour. Each camera was positioned to provide unobstructed, direct visual access to all essential functional areas (Chapter two, Figure 3). The areas included the straw bedded area, the passageway, the isolation pen, the ESF area and the nipple-drinkers. Three hours per day were selected for observation, 08:00-09:00 h, 15:00-16:00 h and 20:00-21:00 h. Observations occurred over one 21-day production cycle from 20th November 2017 to 10th December 2017. The video observations occurred on seven preselected days of the production cycle, including the day before remixing (day 20) and the day of mixing (day 21). The observations continued, on the three consecutive days following a mixing event (days 1,2,3). Days

7 and 14, following remixing, were also selected. Overall, the study provided 21 h of behaviours for analysis.

3.2.2.3. Social behaviours

The behaviour sampling method used an all-occurrences method of observation, considered the most effective and appropriate form of direct sampling method for observing rarer interactions such as positive behaviours (Martin and Bateman, 2007). The approach is consistent with current, related research (i.e., Foris et al., 2018). Every occurrence of preferential associations (Table 4) was documented during the predetermined periods in one production cycle. Preferential associations were determined by socially discriminatory resting partner selection. Observations noted who approached whom to provide a directed network indicating the initiator and receiver of the interaction and if these approaches were tolerated or reciprocated. Due to the use of weighted networks, in which the total frequency of initiated and receiver interactions was observed at an individual level, threshold measures were applied to the preferential association networks. Thresholds were adopted to account for a discriminatory interaction rather than a random encounter (as in Boyland et al., 2016; Davis et al., 2018). Threshold measures are further discussed in detail in the Network threshold filters section. Observations of positive interactions (Table 4) were also recorded, noting the frequency of behaviour, the initiator and recipient of behaviour was also recorded. Thresholds were not applied to the positive behaviours.

Table 4. Ethogram of preferential associations and positive behaviours. Adapted from Durrell et al., 2004; Camerlink et al., 2016a.

Behaviour	Description
Positive behaviours	Any nasal contact between two individuals involving sniffing, nosing, licking without an aggressive reaction or flight.
Preferential Associations	
Social selection of resting partner	Approaching a resting sow and then sitting or lying with physical contact or resting (asleep or awake) to selected sow, separated <1m from the head of selected sow and directly next to her. The proximity of approaching sow tolerated >60s.

3.2.3. Network construction

3.2.3.1. Network threshold filters

Thresholds were applied to the frequency of preferential interactions that occurred between nodes due to the use of weighted data, allowing for the determination of the sustainment of affiliative relationships and discriminatory social selection**.** The application of thresholds to the social networks of preferential associations in the current study was conducted as a measure to overcome any ambiguity as to the presence of preferential associations rather than random interactions, demonstrated in other social network studies (i.e., Boyland et al., 2016; Davis et al., 2018). This present study selected average mean preferential associations and 1.5 x mean thresholds based on direct observations. The filter measure is consistent with other preferential association research of pigs (i.e., Durrell et al., 2004). However, Durrell et al. implemented a threshold set at twice the mean level of interactions; as the current study did not have associations that occurred at this threshold, the application of 1.5 x mean was employed instead.

Three matrices were constructed using the filtering technique; descriptions of the networks are outlined in table 5.

Table 5. Description and threshold levels of preferential associations for the original network (n=78), the mean network (n=70) and the 1.5 x mean network (n=42)

Network composition	Description of network	Threshold measure applied
Original	The original and unfiltered network consisting of all preferential associations, including singular interactions taken over the seven days of observations.	Inclusive of 1-5 interactions between any initiator and the same recipient.
Mean	The mean network consisting of the mean weighted degree of preferential associations taken over the seven days of observations.	Inclusive of 2-5 interactions between any initiator and the same recipient.
1.5 x mean	The 1.5 x mean network consisting of the 1.5 x the mean weighted degree of preferential associations taken over the seven days of observations.	Inclusive of 3-5 interactions between any initiator and the same recipient.

3.2.3.2. Visualisation of the networks

Visualisation of the social networks of preferential associations for all three networks; the original, mean and 1.5 x mean were displayed as sociograms. The original, mean and 1.5 x mean networks consisted of directed ties, in which the initiator and recipient of the preferential association are presented, allowing for the visualisation of 'who approached whom'.

3.2.3.3. Identification of the subgroups

K-cores have been applied to the mean network sociogram to ascertain subgroup based upon connectedness. A *k*-core is a subgraph in which every node has degree *k* or more connections with other nodes within the subgraph (Borgatti et al., 2018). For example, in a 3-core subgraph, nodes will be connected to at least three other nodes, which in turn connect with at least three or more

other nodes. The *k*-core reflects the number of individuals whom a sow connects with; it does not show the frequency of interactions.

3.2.4. Quantifying missing data

Due to the dynamic nature of the herd in the study, all sows were not permanently or consistently present during the 21 h of video recordings observed. The data were weighted to account for the hours that individuals were missing from the study. The coefficient applied to both degree centrality, and betweenness centrality for absent sows is, $y = n/x$.

Where:

y = weighted value of interactions per hour observed

n = value of either degree centrality or betweenness centrality

x = number of hours observed

3.2.5. Data analysis

Matrices of the preferential associations for the mean network were constructed in Excel and imported into Ucinet 6, version 6.634 (Borgatti et al., 2002). Sociograms were created in NetDraw (Borgatti et al., 2002). The general network and individual network metrics analysed in Ucinet included degree centrality, betweenness centrality, centralisation, density, reciprocity, clustering coefficients, *k*-cores, and the E-I index. Statistical analysis was performed in R.3.4.1 (R Development Core Team, 2017). Data were subsequently tested for normality via histograms and the Shapiro Wilks test. The data were found to be nonnormally distributed. GLMMs were performed in R.3.4.1 (R Development Core Team, 2017) using the R package lme4, version 1.1-21

(Bates et al., 2015) to test for differences in behaviour between subgroups and parity. Upon testing, the negative binomial model was found to be the best fit for the probability distribution. For each model, the pig identification number represented the random effects, and fixed effects included subgroup and parity.

3.3. Results

3.3.1. Social tolerance and preferred lying location

To address the issue, that the sows may be tolerating the approach and proximity of one another due to preferred lying location rather than a preferential association, variance in behavioural strategies were analysed in the mean network. 47% (n=33) of the PC1 herd exhibited non-tolerance behaviour when approached by another sow, where an initiated advance was not tolerated beyond 60 seconds. There were no significant differences in the number of received approaches between tolerant and non-tolerant individuals (p = 0.08) however, non-tolerant sows did receive a slightly higher mean rate of preferential associations (7.4 ± 4.1SD) than tolerant sows (5.9 ± 4.4SD). The findings show that there is variance in individual behavioural strategy and that some sows will not tolerate specific individuals regardless of whether they are in a preferred lying location and will either displace themselves or displace the initiator of the behaviour through aggression.

3.3.2. General network-level results

Visualisations for the unfiltered, mean and 1.5 x mean networks are represented by sociograms illustrating preferential associations between herd members over the production cycle. The sociograms show the total number of interactions across the seven preselected days, with 21 hours of observations. The edges between nodes are directed and weighted. Directed interactions illustrate who approached whom, where there is at least one interaction in which proximity was tolerated beyond 60 seconds. All sociograms represent complete and one-mode networks (Figures 5a, 5b and 5c), one-mode networks refer to social networks in which all the nodes are similar to each other (O'Malley and Marsden, 2009). The sociograms highlight that the cohesiveness of the networks declined as the required threshold level of interaction necessary to be included in a specific network increased. Reduced cohesiveness is demonstrated by the increased count of components within each network, with the unfiltered network showing the maximum global cohesion. As an illustration of sociality, the mean network displays the variation between individuals in terms of the number of approaches made. Within the mean network distribution of individuals with higher incoming ties (received preferential associations) are generally shown to be more centrally positioned inside the central core. It indicates there are individuals within the herd who may be preferable to approach.

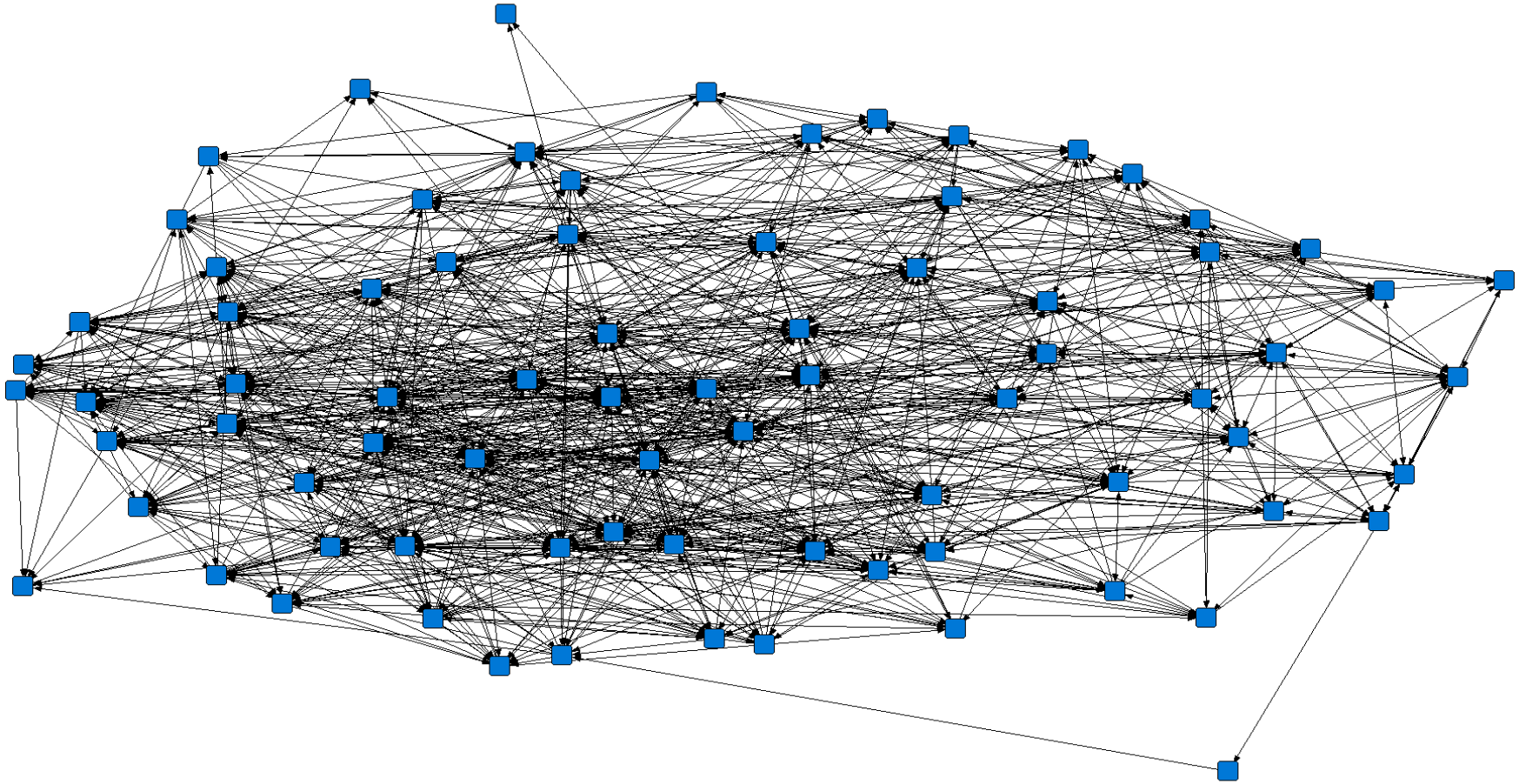

Figure 5a. Directed sociogram of all preferential associations in the original network between dry-housed gestating sows (n=78). Observations occurred at Sturgeons farm, Writtle University College, Essex between 20th November and 10th December 2017.

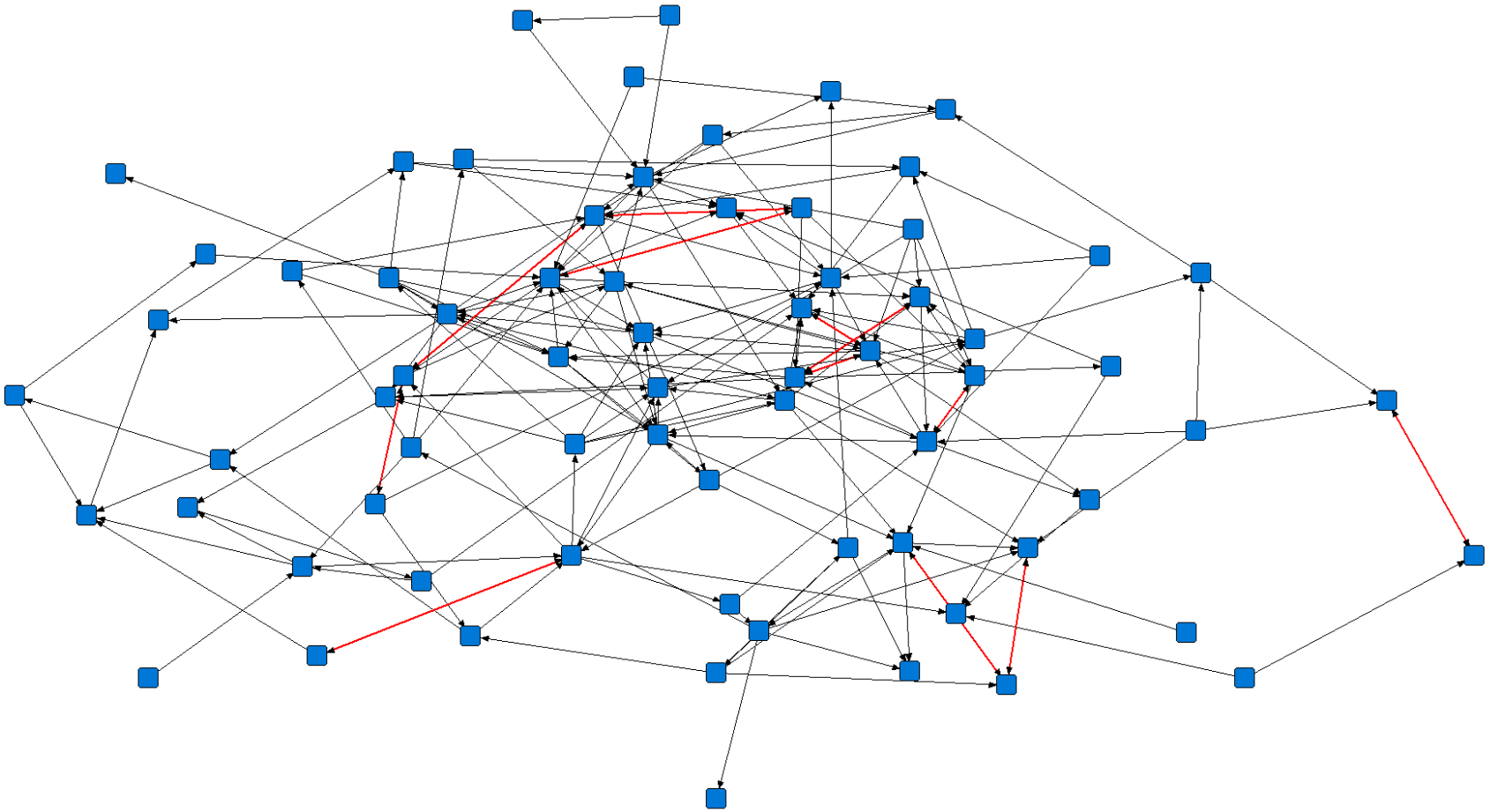

Figure. 5b. Directed sociogram of all preferential associations in the mean network between dry-housed gestating sows (n=70). Observations occurred at Sturgeons farm, Writtle University College, Essex between 20th November and 10th December 2017. Reciprocated ties are shown as a `red` edge.

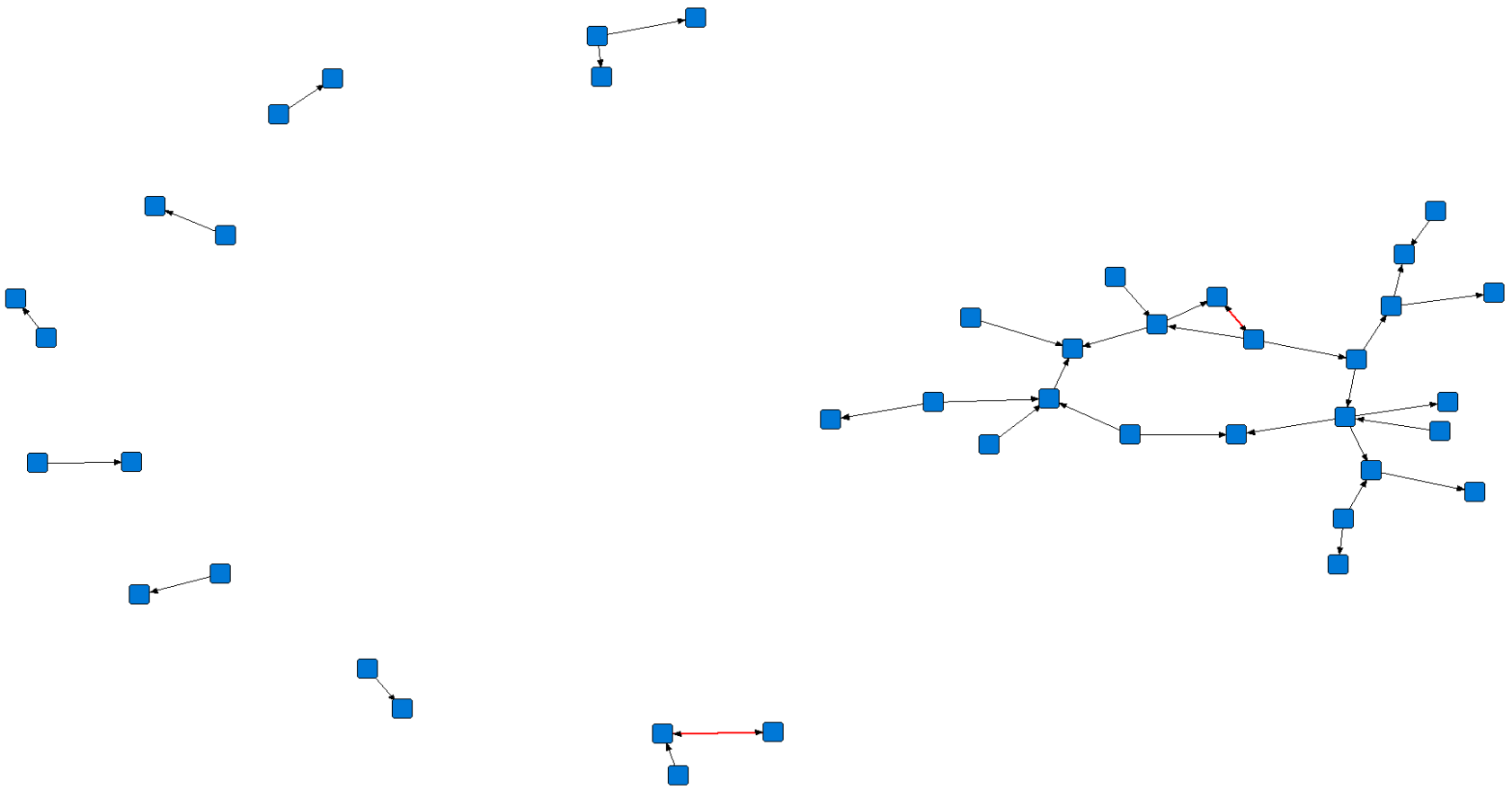

Figure 5c. Directed sociogram of all preferential associations in the 1.5 x mean network between dry-housed gestating sows (n=42). Observations occurred at Sturgeons farm, Writtle University College, Essex between 20th November and 10th December 2017. Reciprocated ties are shown as a `red` edge.

3.3.3. Network measures and structure

Table 6. General network and individual-level properties for the original (n=78), mean (n=70) and 1.5 x mean (n=42) preferential association networks.

	Original network	**Mean network**	**1.5x mean network**
***General properties**:*			
Isolates	0	8	36
Components	1	9	45
Unweighted ties	1007	193	37
Network-level:			
Density	0.17	0.04	0.02
Mean Degree	12.91	5.1	0.88
Centralisation degree	0.14	0.13	0.09
Centralisation In-degree	0.06	0.09	0.05
Centralisation Out-degree	0.04	0.05	0.05
Clustering coefficient	0.231	0.077	0.044
Arc reciprocity	0.264	0.124	0.108
Individual level:			
Mean betweenness	73.99	158.37	3.36
Betweenness std.	59.61	173.36	8.07

Density measures disclosed that a low proportion of all potential preferential associations were present within all three networks, with only 4% and 2% of possible connections made in the filtered networks. Within the 1.5x mean network, the low proportion of preferential links is consistent with the high numbers of isolates, and the pattern of behaviours reveals a marked increase in the number of isolates as the threshold filter level increases. The results indicate a lack of propensity to establish more sustained preferential associations as the threshold for interaction increases and are further supported by the mean degree results. There was also a lack of propensity to initiate positive interactions; in the original network, only 280 counts of positive behaviours were observed over the three-week production cycle. Of the 78 sows in the original network, 92% (n=72) initiated positive behaviours, with an average of only 3.6 interactions for each herd member over the three weeks.

Overall population centralisation for all three networks is extremely low, indicating decentralised networks. However, despite this, comparisons to the average betweenness demonstrate the mean network contains more individuals with greater prominence than in the other two networks. All networks demonstrate variation in betweenness values, as indicated by the large standard deviation. Results from the mean network also showed a lot of betweenness variation between the individual actors, indicating that there are individuals with more significant influence than conspecifics within the herd

Reciprocity of all initiated preferential associations in all three networks does not notably deviate from the density levels, suggesting that a high proportion of reciprocated ties may be randomly occurring. Nevertheless, as reciprocity values are slightly above 0, there is the existence of a small number of mutual connections within all three networks, demonstrated in figures 5b and 5c. Additionally, the clustering coefficients indicate little closure between triadic interactions and the coefficients hardly differ from density in all three networks, suggesting that the preferential ties between any two given individuals in the herd are weak with little transitivity occurring.

Despite a lack of cohesiveness and clustering demonstrated in all three preferential association networks overall, the application of *k*-core measures to the mean network reveals the presence of four interconnected core areas (Figure 6). The mean network was selected as it demonstrated the network with the highest mean betweenness and centralisation indegree, indicating a network with potentially more prominent pigs. The maximal subgroup (K4) reflects the most cohesive region of the network, although the subgroup (K3) represents the largest group of connected individuals (n=29). Two further *k*-cores are located on the periphery, albeit

consisting of a much smaller number of nodes. The *k*-cores demonstrate the connectivity of individuals within the herd, yet sociability cannot be inferred from figure 5a as visually weighted ties would be difficult to decipher. A distinction must be made between connectedness and sociability as they may not be synonymous characteristics, and connectedness alone may not account for social influence within the herd. Therefore, differences in sociability represented as the levels of initiated and received preferential associations for individuals, within and between different *k*-cores will be analysed further.

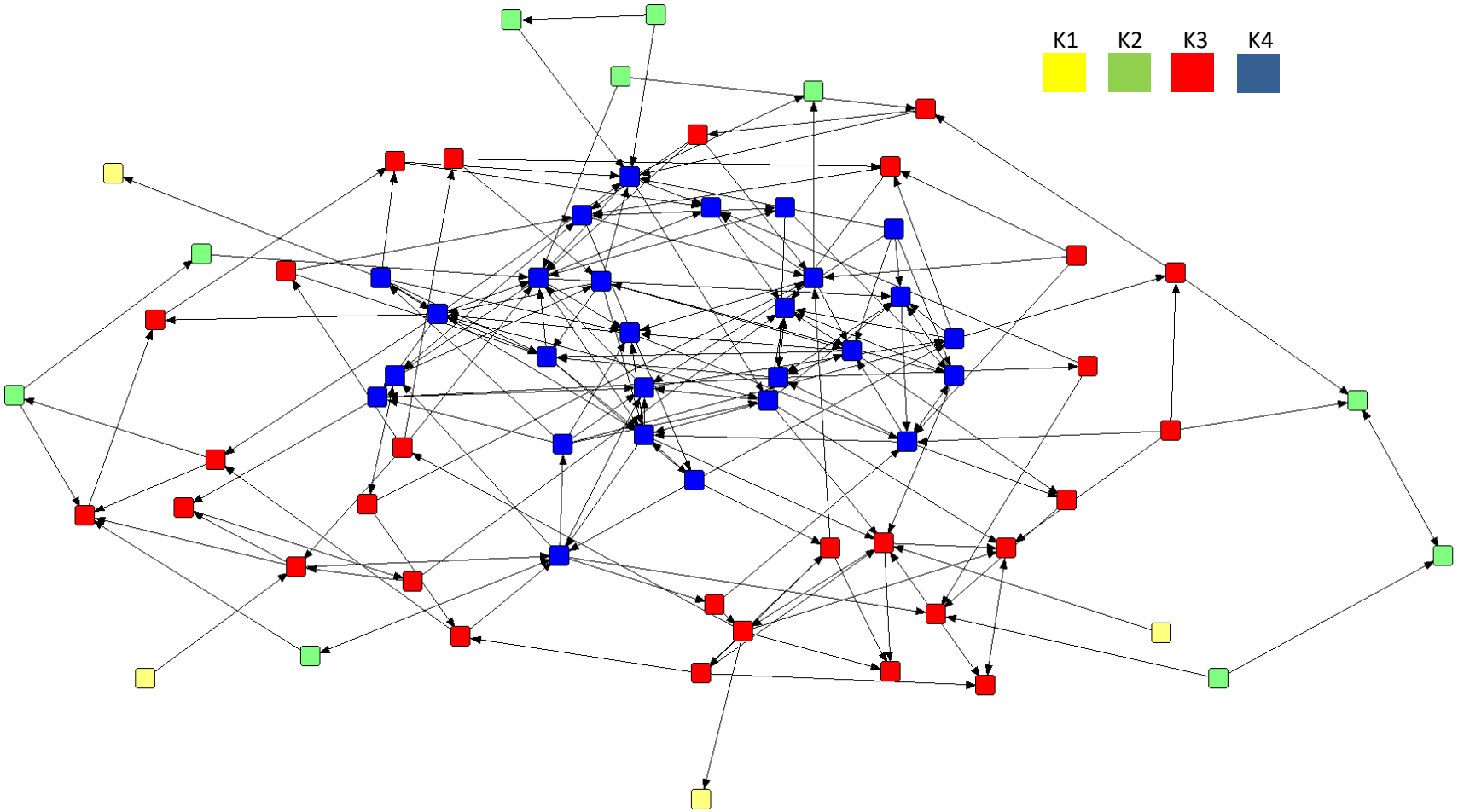

Figure 6. Mean network directed sociogram (n=70) of preferential associations with the *k*-cores analysis applied, showing the formation of subgroups within the herd including K4 (n=27), K3 (n=29), K2 (n=10) and K1 (n=4). A normal distribution is shown with the highest *k*-values representing the most cohesiveness region of the sociogram. Legend denotes k steps for each subgroup. The *k* values, i.e., K4, refer to the subgroup, the coreness value indicates the number of nodes an individual is connected. For example, in K3, an individual is connected to at least three other individuals and those in turn connect with at least three or more other nodes.

The ego-alter similarity of defined attributes within the mean network was measured using the application of the E-I index (10000 permutations). No constraints were observed for the given density or group size for each attribute, so the re-scaled index E-I is not reported. For each attribute, the maximum E-I value is 1 (perfect heterophily) and the minimum E-I value -1 (perfect homophily). Parities ranged from one to seven, breeding groups (1-7) were organised based on farrowing data, and *k*-cores ranged from K1-K4. Results are listed in table 7.

Table 7. Mean network results for preferential associations and ego-similarity for parity, breed group and *k*-core. Internal ties refer to received preferential approaches and external ties refers to initiated preferential approaches.

	Internal ties	**% Internal ties**	**External ties**	**% External ties**	**Expected E-I Index**	**E-I Index**	**Std error**
Parity	130	35.9	232	64.1	0.481	0.282	0.069
Breed Grp	118	32.6	244	67.4	0.696	0.348	0.051
***K*-core**	248	68.5	114	31.5	0.331	-0.370	0.070

Results show that there is a propensity for external ties within the parity and breeding group categories, with an increased inclination towards internal ties for the attributes of a *k*-core subgroup. There is little deviation between the observed E-I index and the expected E-I index for parity and breeding group, supported by the standard error (the value to which the E-I index will vary by chance between the permutation sampling distributions). The lack of deviation and positive values demonstrates that ego-alter associations are not motivated by similarities of parity or familiarity through a breeding group. By comparison, associations do appear to be driven by *k*-core subgroup, as the E-I index deviates more significantly from the expected outcome. Relative comparisons to the standard error suggest a rejection of the null hypothesis, with results appearing to be less random for associations between members of the same subgroup, this

finding is supported by the results of the random permutations test which showed associations based upon *k*-core were not occurring by chance ($p < 0.05$).

3.3.4. Individual-level results

3.3.4.1. Sociability and subgroups

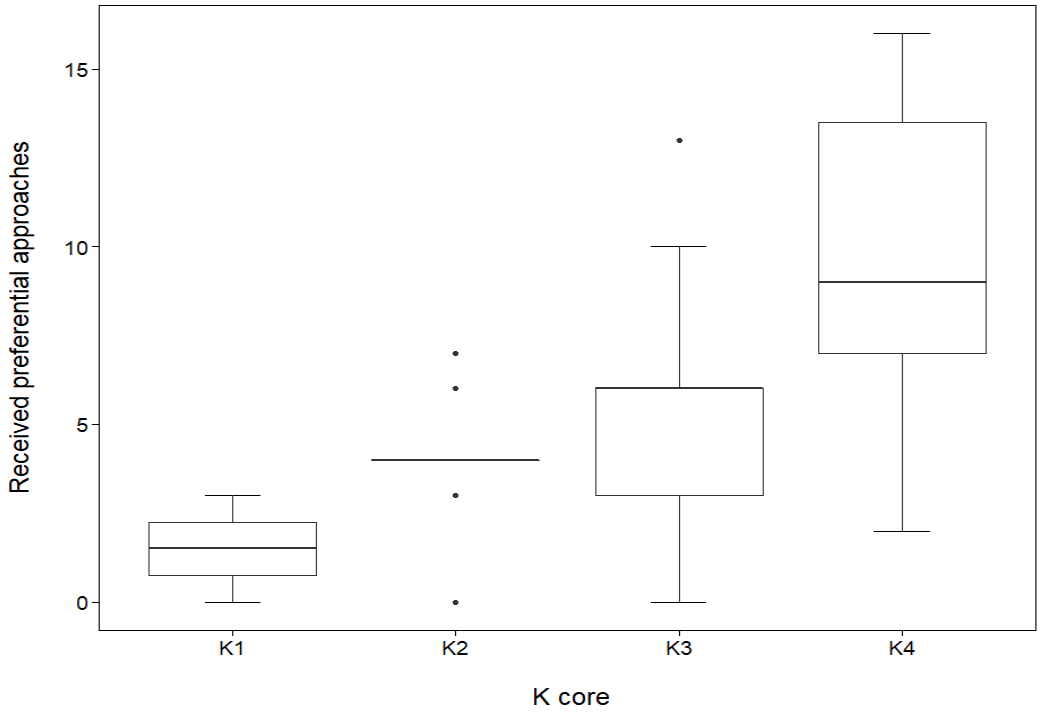

Figure.7a. Distribution of received preferential associations between k-cores in the mean network. Indegree centrality quartiles for all four subgroups (n=70). Sows quantified in K1 (n=4) had a median indegree value of 1.5. The maximum K1 indegree centrality was 3 with a minimum value of 0, giving a range of 3. Sows quantified in K2 (n=10) had a median indegree value of 4. The maximum K2 indegree centrality was 7 with a minimum value of 0, giving a range of 7. Sows quantified in K3 (n=29) had a median indegree value of 6. The maximum indegree centrality was 13 with a minimum value of 0, giving a range of 13. Sows quantified in K4 (n=27) had a median indegree value of 9. The maximum in degree centrality was 16 with a minimum value of 2, giving a range of 14. Significant differences were found in the indegree centrality between k-cores, with individuals in K4 receiving higher levels of preferential associations than conspecifics in other subgroups, $p < 0.01$). The *k* values, i.e., K4, refer to the subgroup, the coreness value indicates the number of nodes an individual is connected. For example, in K3, an individual is connected to at least three other individuals and those in turn connect with at least three or more other nodes.

K-core has a significant effect on the number of received preferential approaches that are occurring between subgroups (Figure 7a). Individuals within K4 received, on average, 9.7 ± 4.2SD

preferential approaches, significantly higher than those in K1 at 1.5 ± 1.3SD, K2 at 4.0 ± 1.8SD, and K3 at 5.4 ± 3.10SD (coef. 0.58, z 4.4, $p < 0.01$). Results also show that the sociability of an individual has a significant effect on *k*-core (Figure 7b). Sociability is measured by the frequency of initiated preferential approaches made by an individual, including preferential approaches extending to sows within other subgroups. Individuals within K4 made, on average, 10.4 ± 5.1SD initiated preferential approaches, significantly higher than those in K1 at 0.8 ± 1.5SD, K2 at 3.0 ± 2.9SD and K3 at 5.2 ± 3.5SD (coef. 0.72, z 4.2, $p < 0.001$).

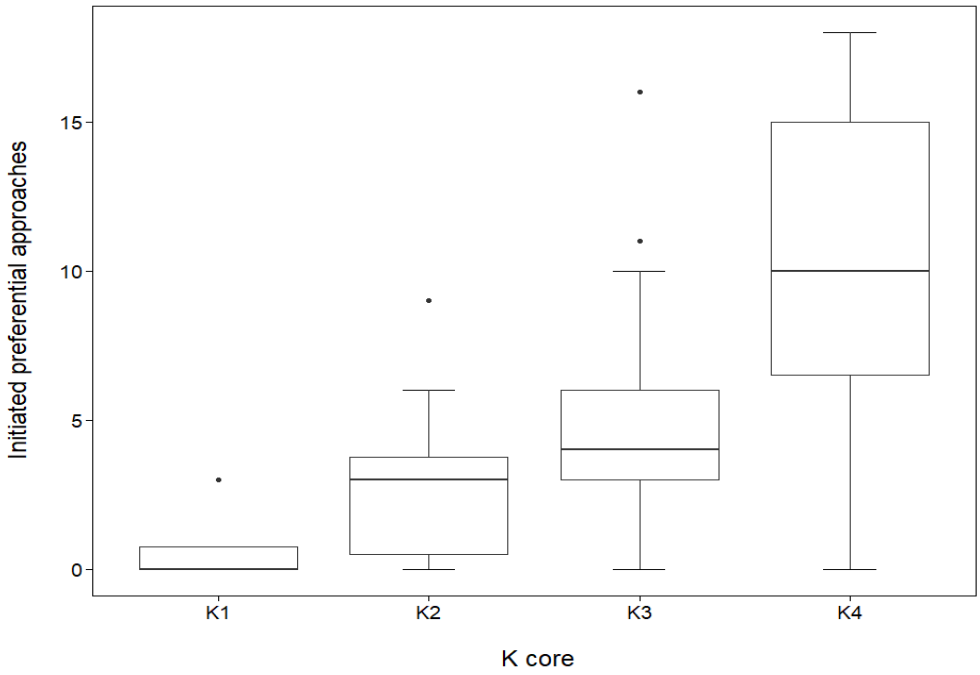

Figure 7b. Distribution of initiated preferential associations in the mean network. Outdegree centrality quartiles (based on preferential associations) for all four subgroups (n=70). Sows quantified in K1 (n=4) had a median outdegree value of 0. The maximum K1 outdegree centrality was 3 with a minimum value of 0, giving a range of 3. Sows quantified in K2 (n=10) had a median outdegree value of 3. The maximum K2 outdegree centrality was 9 with a minimum value of 0, giving a range of 9. Sows quantified in K3 (n=29) had a median outdegree value of 4 The maximum outdegree centrality was 16 with a minimum value of 0, giving a range of 16. Sows quantified in K4 (n=27) had a median outdegree value of 10. The maximum outdegree centrality was 18 with a minimum value of 0, giving a range of 18. Significant differences were found in the outdegree centrality between *k*-cores, with individuals in K4 receiving higher levels of preferential associations than conspecifics in other subgroups, $p < 0.001$). The *k* values, i.e., K4, refer to the subgroup, the coreness value indicates the number of nodes an individual is connected. For example, in K3, an individual is connected to at least three other individuals and those in turn connect with at least three or more other nodes.

3.3.4.2. Sociability and parity

There were no significant differences in the frequency of initiated or received preferential approaches and parity. Results indicate that parity is not a predictor of the popularity or sociability of an individual based upon a network of preferential associations.

3.4. Discussion

The topic of whether commercial sows form preferential associations remains unclear, a result of the caveat revealed in other related studies (Durrell et al., 2004; Goumon et al., 2020), in which preferred social selections and environmental preferences, or constraints cannot indisputably be differentiated between. The application of threshold measures within preferential association networks goes some way to rule out random interactions, however, in the current study repeated interactions were occurring at a low level. It may be expected that some sows would be more connected than others, and this may be determined by accessible lying areas. For example, subordinate sows may have no choice but to locate in the least desirable area, which may wrongly be perceived as preferential associations with sows already at rest. Despite this, coreness value did influence the number of interactions initiated and received at a level of significant difference between individuals in each of the four subgroups. Sows in the highest connected subgroup were preferable for approach then their lower connected conspecifics, indicating a level of social discriminatory behaviour.

The application of sociograms and network measures show that all three networks reflected a lack of cohesiveness, demonstrated by low-density results (Table 6). As the threshold for

preferential interactions increased, the proportion of all possible dyadic ties decreased, with only 4% and 2% of potential connections made in the mean and mean x 1.5 networks, respectively. The networks were one-mode networks, thus, allowing each sow the opportunity to interact with all other sows within the herd. Additionally, sows were confined to the straw bedded area (130m^2) for a maximum of one hour, three times a week, while husbandry tasks were completed. As stocking density during this time would increase, affecting proximity boundaries between individuals, it could be expected that density levels would be higher. The findings of this study are consistent with previous research, continuing to show that affiliative interactions within commercial systems are rarer than agonistic interactions (Foris et al., 2018). An expected result, as stocking density in commercial groups, will impact upon the formation of aggressive behaviours (Estevez et al., 2007). Investing in the creation of affiliative connections may be less rewarding than investing in agonistic interactions, particularly within dynamic systems.

The greatest cohesiveness was observed within the unfiltered network, albeit with a density level of 0.17, a result of the inclusion of ties that occurred only once. Single ties suggest randomness in the preferential selection, yet it is difficult to differentiate between extrinsic or intrinsic motivations for approaching other pigs. Extrinsically, lying together is an essential function in social groups, particularly in pregnant sows which have a lower critical temperature (14˚C) due to feeding restrictions (Andersen et al., 1999). However, as the threshold for interactions increased within the filtered networks, it was recorded that some sows returned to the same individual up to five times, supporting the findings that there is variance in individual behavioural strategies. This behaviour is potentially a strategy that demonstrates intrinsic motivation that extends

beyond the necessity for thermoregulation and challenges the social indifference concept to lying partners observed in other commercial species (Abeyesinghe et al., 2013). The stocking density in the dry barn is variable, a result of a dynamic system; approximately 2.32m² per sow (assuming on average there is a minimum of 56 sows), as the farrowing unit can hold 24 pigs. Space allowance is in line with the recommendations of 2.25m² of the Red Tractor Assurance guidelines for pigs (Assured Food Standards, 2014) and sows have free movement within the barn of all the functional areas. Therefore, the opportunity to perform avoidance behaviour is available if so desired. By contrast, freedom of movement also allows for social discrimination in preferential associations. Despite the presence of apparent discriminatory behaviour, a comparison of the mean degree between networks reflects a lack of propensity to establish more sustained preferential associations as the threshold for interactions increased.

An explanation for this lack of sustained preferential associations lies with reciprocity and the costs, and benefits involved in engaging in prosocial behaviours. Firstly, prosocial behaviours are recognised as those social behaviours that are positive to both the initiator and recipient (Rault, 2019). Rault further categorised prosocial behaviours as; caregiving, affiliation, sharing, social teaching, cooperation and behaviours that extend to benefit the whole group, such as predator defence. Unlike many other social species, though, commercial adult pigs have a more limited repertoire of behaviour. These limitations do not allow for engagement of specific prosocial behaviours, such as allogrooming or social play, which are proven to create higher degrees of sociality. For example, social licking in weaned dairy cows has been determined to strengthen social relationships (Veissier and Le Neindre, 1989), while social play correlates to social tension

reduction in captive primates (Yamanashi et al., 2018). Secondly, reciprocity values of preferential ties were low in the present study and varied little between the networks. Thus, suggesting that these affiliative approaches (even at higher thresholds) were not mutually beneficial, despite the proximity of the initiator being tolerated. Voelkl (2015) supports this suggestion and states that; '*In order to reciprocate an individual needs the ability to recognise and memorise that it has received help from another individual*'. In other words, if the recipient sow of the affiliative approach does not deem that interaction to 'be helpful', then the tie will not be bidirectional. Furthermore, indicating that reciprocation of affiliative behaviours is not observed to be a motivator for approaching the 'popular' pigs.

The clustering coefficient results of all three networks demonstrate that little transitivity is occurring and that the ties that exist between individuals are weak. Triadic closure occurs when there are two strong ties between individuals; based upon the concept that friends of friends will also become friends (Mollenhorst et al., 2011). Brent (2015) suggested that these indirect relationships play an essential role in animal behaviour and sociality. Conversely, the formation of strong bonds does present certain social limitations, demonstrated in Granovetter's (1973) 'strength of weak ties' concept. Granovetter proposed that weak ties allow access to new information from different parts of the social network that would not be reached through the formation of only strong ties or friendships. That in fact, strong friendships can limit interaction with other less familiar actors within a network. When applied to animal behaviour, research has shown that establishing weak ties can have a positive effect on fitness-related benefits. McFarland et al. (2017) found that wild female chacma baboons (*Papio ursinus*) that formed weak ties had a

greater offspring survival rate. Additionally, the existence of weak structural balance within the herd is consistent with the dynamic and unstable nature of the environment, where triadic ties are weak. Previous network studies have demonstrated that dynamic systems cause social imbalance due to a failure to engage in indirect 'friendships', both in ungulates and other mammalian species. Ilany et al., (2013) reported that newly introduced rock hyrax (*Procavia capensis*) formed unbalanced triads resulting in social instability, while the dynamic nature of onager (*Equus hemionous*) society results in structural imbalance (Sundaresan et al., 2007).

Overall centralisation for all three networks was extremely low, and therefore the herd can be deemed as a decentralised social group (Ramos et al., 2019). Results are consistent with previous research into network development and characteristics in pigs (Büttner et al., 2015). Nevertheless, despite an apparent absence of leaders within the herd; considerable variations in individual betweenness scores suggest some specific sows have greater prominence and power. It is particularly true in the mean network which demonstrated the highest mean betweenness, therefore this network was taken forward for analysis. The mean network and *k*-core sociogram (Figure 5b) shows that despite a lack of centralisation, there is a degree of social structure within the herd, indicating that pigs are not socially equal. Individuals within the most cohesive region of the network (K4) had significantly higher rates of incoming ties than other herd members. They had, on average, 9.44 incoming ties compared to K3 (4.83 ties) and K2 (3.7 ties). Sows that lay on the periphery of the network (K1) were far less attractive to other sows with only an average of 1.25 incoming ties. These findings reveal that the number of connections impacts upon popularity and approachability, even when these incoming ties are not reciprocated. Also, the sociability of

an animal was seen to affect social position, with sows in K4 initiating significantly higher rates of external ties. Sows in K4 made, on average, 10.04 approaches compared to those in K3 (4.74) and K2 (2.8). Again, it was found that the least popular pigs in K1 were also the least sociable, initiating only an average of 0.5 approaches. Zemljic and Hlebec (2005) cite that, '*actors who are the initiators of behavioural interactions are network influencers and actors who are the recipients provide a measure of support*'. It can, therefore, be concluded that individual sociability determines the formation of the social structure. Plasticity in behaviour could improve social standing in the group and increase potential rewards, as demonstrated in the Jones et al., (2012) social network study on the influence of unpredictable feeding schedules on social roles in Atlantic salmon.

Finally, In the present study homophily was not present based upon the traits of parity or familiarity (breeding group). It must be noted though that the parity results may have been influenced by a lack of distribution between parity groups; mid-parity sows dominated the herd. Despite this, investigations of associations based upon such traits have shown conflicting results in previous research. Hoy et al. (2009b) found that younger sows demonstrated homophily while forming groups, however, Durrell et al., (2004) contrasted this result, reporting no significant correlation between preferential associations and weight, familiarity, and relatedness in pigs. The lack of relationship between the selected traits and homophily is supported by the revelation that parity does not impact upon the centrality metrics when based upon preferential associations.

3.5. Conclusions

This work reveals that the sociability and connectedness of individual sows within the herd influences the group dynamics and social structure. The key findings show that despite low centralisation at the group level, indicating social equality, there are sows who have more significant influence and prominence at the individual level than their subgroup conspecifics. This social inequality is seemingly determined by connectedness (*k*-core) and sociability. These individuals do not have to reciprocate preferential behaviours to continue to be more approachable to other less connected pigs. The lack of reciprocation and homophily of traits demonstrates that 'friendships' may not develop in dynamic systems of breeding sows. There is the propensity, however, to offer transient social support motivated by other mechanisms, even when this support is one-directional. Individuals within the herd have the potential to alter their social role through behavioural plasticity, although personality may impact this. The current study begins to give insight into how understanding the impact of individual behaviour on a social structure can be applied to management strategies, such as manipulation of group composition and breeding programmes. Finally, social complexities and individual differences in behavioural strategy may hinder the future success of solutions to reducing aggression in a dynamic commercial herd. Further understanding the variations and stability of social prominence, and influence in the network is a crucial step for enhancing this research and will be explored in chapter four.

Chapter four:

Social prominence and influence in a dynamic breeding sow herd in three preferential association networks

4.1. Introduction

The identification of critical individuals presents an opportunity to gain a more in-depth understanding of social structure within a network, building upon current knowledge of the impact of individual differences in network position (Totterdell et al., 2008). In chapter three, it was demonstrated that all pigs are not equal because the complexities in the formation of social networks are dependent on individual behavioural patterns and interactions. Subsequently, the structure of the social network can affect the direct and indirect interactions, determined by individuals in positions of increased power or connectedness through social influence and prominence. Socially prominent individuals are those who engage in significantly higher levels of social interactions than conspecifics. Socially influential individuals are those who have a significantly higher ability to broker or transfer behaviour, disease, or information than conspecifics.

Investigations of network position present a potential mechanism for assessing and monitoring health and behavioural stability in commercial species (de Freslon et al., 2019). Individual variation in behavioural patterns can both negatively and positively impact upon a network, and the capacity to identify key individuals is pivotal for the application of positive changes or interventions. Socially central and highly connected individuals are shown to be at greater risk of infection and present as a source for faster disease and parasite transmission (Christley et al., 2005; Sintayehu et al., 2017; Bieber et al., 2019; de Freslon et al., 2019). Furthermore, understanding how cascades of aggression move through a network is essential for improving

welfare and controlling agonistic behaviours. For example, Jones et al. (2010) found that changing feeding schedules in Atlantic salmon, *Salmo salar*, altered social roles, with fish becoming either an initiator or receiver of aggression. Flack et al. (2006) identified key individuals in a pig-tailed macaque group, *Macaca nemestrina*, responsible for maintaining social cohesiveness through policing behaviour to reduce aggression. Removal of these key individuals was found to increase aggression significantly within the group. In contrast, in some social groups, the retention of highly connected animals can contribute to chronic aggression (Foister et al., 2018). Cohesiveness and group fitness are also affected by the ability to transfer information for social learning effectively and resource allocation (Boesch, 1991; McComb et al., 2001).

Decentralised societies, in which there are not clearly defined key individuals, present more significant challenges for identifying social influence in behavioural research (Flack et al., 2005). The dynamic mixing practices and ephemeral groupings of intensive pig farming highlight the complexities for identifying socially prominent and influential individuals due to the social instability (Parent et al., 2012; Büttner et al., 2015). Social network analysis (SNA) is an established framework (Davis et al., 2018) for modelling intricate patterns of social interactions and investigating the impact of subtle behavioural nuances in both stable and dynamic social groups. This method enhances understanding of which animals may be more prominent or influential in a network by applying SNA metrics at a group and individual level of analysis (Makagon et al., 2012). Social roles include the key players (Croft et al., 2008) including individuals who have a positive or negative influence (Makagon et al., 2012) or are socially central (Kulahci et al., 2018b). Social roles also include social hubs, individuals more highly connected than conspecifics (Verdolin et al., 2014)

and social bridges, individuals that connect previously unconnected conspecifics (Verdolin et al., 2014).

Lusseau and Newman (2004) conducted an initial study utilising SNA for the research of animal behaviour. The study found that although there was a decentralised population within a network of Bottlenose dolphins, *Tursiops truncatus*, they identified a small proportion of crucial players. These key dolphins acted as social brokers enabling greater cohesion between the sub-communities that had developed. Social brokerage is a measure of influence ascertained by SNA. It shows the ability of individuals to fill structural holes within a social network (Burt, 1992) by employing the SNA metric of betweenness centrality. Betweenness centrality is an essential measure of influence in animal societies; as it is the only mechanism for establishing links between unconnected individuals in a network (Stovel and Shaw, 2013). Additionally, the SNA metric of degree centrality identifies prominent individuals by measuring the frequency of interactions (Makagon et al., 2012). The employment of SNA has enabled behavioural research into the role of central individuals in several wild species (Ramos-Fernández et al., 2009; Gero et al., 2013; Verdolin et al., 2014).

The SNA metrics for identifying social influence and prominence are currently under-utilised for addressing welfare and production issues in commercial animals, the metrics have been predominantly applied to non-domestic species. All despite its significance as a mechanism for further understanding how network position may have individual and group level fitness consequences (Naug, 2008; Wilson et al., 2013; Bieber et al., 2019). Furthermore, little is known

about the changes in prominence or influence over time (Chen et al., 2014). An enhanced insight would be a valuable commodity, particularly in commercial systems in which predictive models of productivity and welfare, based upon our understanding of social individuality would be economically significant. This study will seek to identify socially prominent and influential individuals in the dynamic, preferential association networks of dry breeding sows, by employing SNA metrics to investigate the distribution of these strategic positions throughout the herd's social structure. The study will look at the inter and intra individual variation across three production cycles to address the research question of stability in prominence and influence. The effect of parity on social prominence and influence will be explored, an evaluation of the impact of time spent in the network will also be made due to the herd's dynamic nature.

4.2. Methods

Chapter two provides a detailed description of the methods. A summary is outlined in the following sections:

4.2.1. Animals and housing

The study was conducted at Sturgeons farm, Writtle University College, Chelmsford, Essex between November 2017, and January 2018. The study group consisted of a commercial cross of Large White-Landrace and Pietrain breeds; parities one to seven, housed in a dry sow barn. Sows were fed on a complete feed for breeding sows through electronic sow feeders, reset daily at 15:00 h, with additional access to *ad libitum* straw. Sturgeons Farm operates a dynamic system in

which small groups of sows are remixed into the main herd every third Tuesday. There is a repeated cycle of production following the pattern, farrowing week, breeding week, and weaning week. For individual identification, each sow was marked with coloured dots, stripes, or both on their backs. Colour codes corresponded to ear-tag number.

4.2.2. Data collection

4.2.2.1. Sow data

The farm diaries and liaison with the pig unit manager provided relevant information concerning parity, farrowing date, date of remixing and remixing group.

4.2.2.2. Video observation data

A total of five CCTV H.265 4Mega Pixel Eyeball PoE, infrared Dome cameras were installed in the dry barn to capture and observe sow behaviour. Each camera was positioned to provide unobstructed, direct visual access to all essential functional areas (Chapter two, Figure 3). The areas included the straw bedded area, the passageway, the isolation pen, the ESF area and the nipple-drinkers. Three hours per day were selected for observation, 08:00-09:00 h, 15:00-16:00 h and 20:00-21:00 h. Observations occurred over three 21-day production cycles from 20th November 2017 to 21st January 2018. The video observations occurred on seven preselected days of each production cycle, including the day before remixing (day 20) and the day of mixing (day 21). The observations continued, on the three consecutive days following a mixing event (days 1,2,3). Days 7 and 14, following remixing, were also selected. Hereafter production cycle one, production cycle two and production cycle three will be referred to as PC1, PC2 and PC3,

respectively. Overall, the study included 21 h of video footage for each production cycle providing 63 h of behaviours for analysis.

4.2.2.3. Social behaviours

All occurrences of preferential associations were recorded using video observations to establish the frequency of the defined behaviour (Chapter three, Table 4). Preferential associations were observed to establish the presence of social discrimination. The social selections of resting partners were determined by recording who approached whom to rest with over time and if these approaches were tolerated and reciprocated. The initiator and receiver of each behaviour were recorded to enable directional ties to be identified during the analysis. Threshold measures were applied to each network to account for a preferential association rather than a random interaction, with the mean number of prosocial advances calculated for the 21 hours of observations in each production cycle**.** For all production cycles, the threshold measure was inclusive of ≥ 2 preferential interactions between an initiator and the same recipient.

4.2.3. Network construction

4.2.3.1. Visualisation of the network

Visualisations of the social networks for preferential associations in all three production cycles were shown as sociograms. The networks consist of directed ties, in which the initiator and recipient of the preferential association are displayed, allowing for the visualisation of 'who approached whom'. Although edges are not weighted in the sociograms, all networks recorded the frequency of indegree centrality (received ties) and outdegree centrality (initiated ties).

4.2.3.2. Identification of subgroups

K-cores have been applied to the preferential association networks in each production cycle to ascertain subgroup based upon connectedness. A *k*-core is a subgraph in which every node has degree *k* or more connections with other nodes within the subgraph (Borgatti et al., 2018). For example, in a 3-core subgraph, nodes will be connected to at least three other nodes, which in turn connect with at least three or more other nodes. The *k*-core reflects the number of individuals whom a sow connects with; it does not show the frequency of interactions.

4.2.4. Identifying socially prominent and influential sows

4.2.4.1. Quantifying social prominence in the preferential association networks

Degree centrality can provide a measure of prominence within subgroups (Gero et al., 2013). Prominent animals with a significantly higher degree centrality than their conspecifics are consequently more highly connected (Verdolin et al., 2014). Within the preferential association networks in the three production cycles, sows with a combined indegree and outdegree centrality above the 95% range of degree centralities for their *k*-core subgroup quantified as socially prominent (adapted from Verdolin et al., 2014). Hereafter, quantified sows are referred to as socially prominent sows (SPS), and a sow not quantified SPS is referred to as non-SPS.

4.2.4.2. Quantifying social influence in the preferential association networks

Betweenness centrality can provide a measure of influence within and between subgroups (Lusseau and Newman, 2004). Individuals with a significantly higher betweenness centrality than their conspecifics are subsequently more influential. Within the preferential association networks

in the three production cycles, sows with a betweenness centrality above the 95% range of betweenness centralities for their *k*-core subgroup quantified as socially influential (adapted from Verdolin et al., 2014). Hereafter, socially influential sows will be referred to as SIS, and a sow not quantified as SIS will be referred to as non-SIS.

4.2.4.3. Coefficient for quantifying SPS and SIS in the preferential association networks

Socially prominent and influential sows either identified as those individuals whose centrality metrics fell outside the range of 95% of degree centrality, betweenness centrality or both for their assigned subgroup (*k*-core). This method is consistent with previous social network research (i.e., Verdolin et al., 2014). These individuals quantified applying the following coefficient, $x \pm z * s/ \sqrt{n}$. Where:

x = Mean degree centrality or the betweenness centrality for the *k*-core

z = 1.96, for the 95% confidence interval

s = Standard deviation of the degree centrality or the betweenness centrality for the *k*-core

$\sqrt{n}$ = Square root of the *k*-core population total

4.2.5. Data analysis

Matrices of the preferential association networks for each production cycle were constructed in Excel and imported into Ucinet 6, version 6.634 (Borgatti et al., 2002). Sociograms were created in NetDraw (Borgatti et al., 2002). The general network and individual network metrics analysed in Ucinet included degree centrality, betweenness centrality, centralisation, and *k*-cores. Statistical analysis was performed in R.3.4.1 (R Development Core Team, 2017). Data were subsequently

tested for normality via histograms and the Shapiro Wilks test. The data were found to be nonnormally distributed. GLMMs were performed in R.3.4.1 (R Development Core Team, 2017) using the R package lme4, version 1.1-21 (Bates et al., 2015) to test for changes in social network metrics between production cycles, differences in network metrics and time spent in the herd, and the effect of parity on social prominence or influence. Upon testing, the negative binomial model was found to be the best fit for the probability distribution. For each model, the pig identification number represented the random effects, and fixed effects included mixing group, parity, and production cycle.

4.3. Results

4.3.1. Visualisation of the network: Socially prominent and influential sows

Sociograms illustrate the preferential associations between sows over PC1, PC2 and PC3. The sociograms display the total number of preferential association interactions across seven preselected days, with a total of 63 hours of behavioural observations recorded. The edges between nodes are directed and weighted. Tolerated behaviour beyond 60s, is illustrated in the directed interactions, showing who approached whom. The sociograms represent complete and one-mode networks.

The sociograms in figures 8a, 8b and 8c illustrate the numbers and distribution of socially prominent sows (SPS) and socially influential sows (SIS) within all three networks. In PC1 (n=70) 30% (n=21) of the total population were quantified as SPS and 19% (n=13) were quantified as SIS.

29% (n=6) of SPS also identified as SIS. In PC2 (n=52) 37% (n=19) of the population quantified as SPS and 21% (n=11) quantified as SIS. 53% (n=10) of SPS were identified as SIS. Finally, in PC3 (n=56) 30% (n=17) of the population quantified as SPS and 11% (n=6) identified as SIS. 24% (n=4) of SPS also identified as SIS in PC3. Results are outlined in Table 8.

Table 8. An overview of the number of sows quantified as either socially prominent or influential in production cycle 1, production cycle 2 and production cycle 3 in the preferential association networks.

	Production cycle 1 N = 70	Production cycle 2 N = 52	Production cycle 3 N = 56
Socially prominent sows (SPS)	21	19	17
Socially influential sows (SIS)	13	11	6
Both SPS and SIS	6	10	4

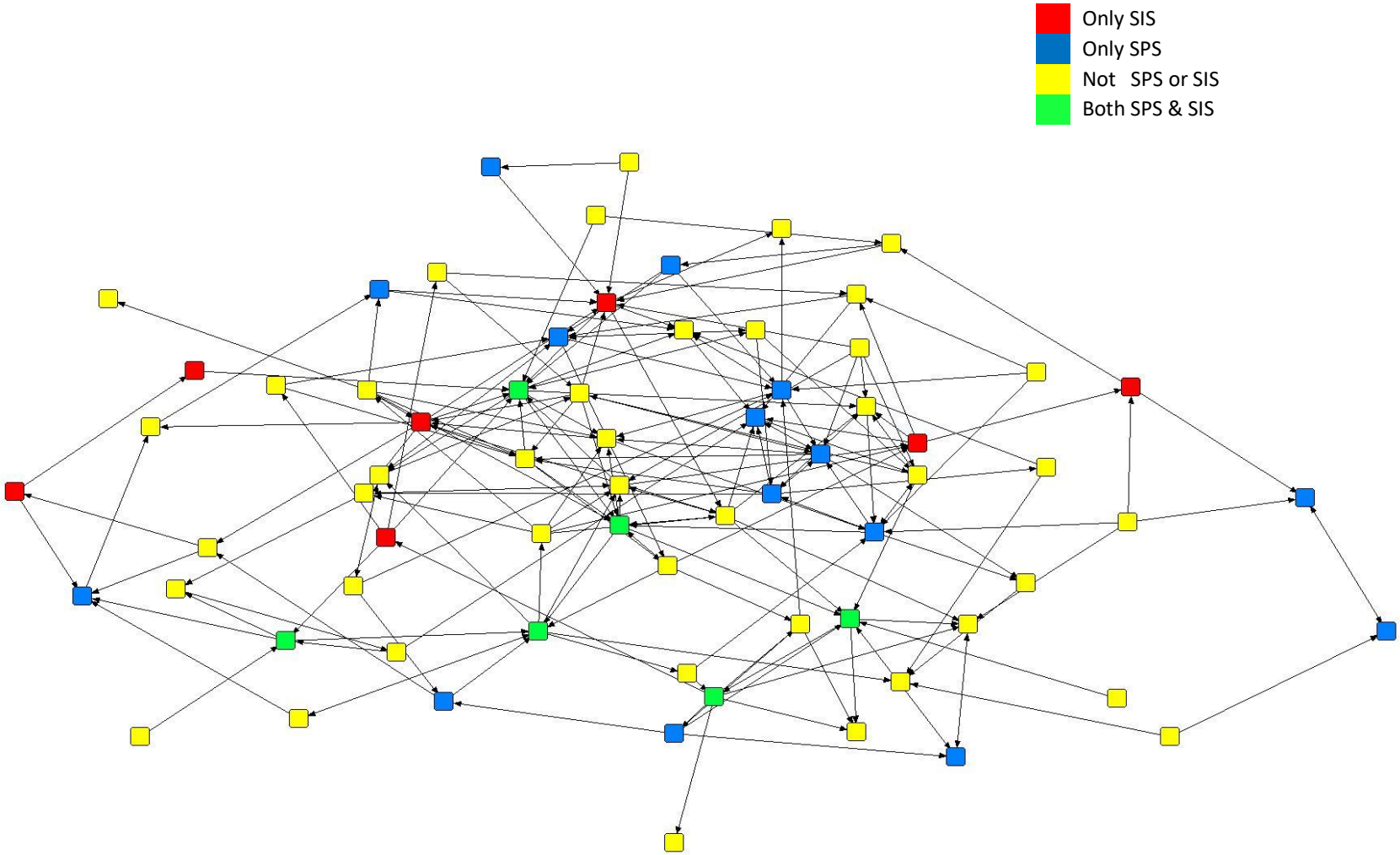

Figure 8a. Directed sociogram of preferential associations between dry-housed gestating sows for production cycle 1 (n=70). Behaviours occurred at Sturgeons farm, Writtle College, Essex between 20th November and 10th December 2017. Sociogram shows sows quantified as only socially prominent (Only SPS, n=15), only socially influential (Only SIS, n=7), both socially prominent and influential (Both SPS & SIS, n=6) or not socially prominent or influential (Not SPS or SIS, n=42).

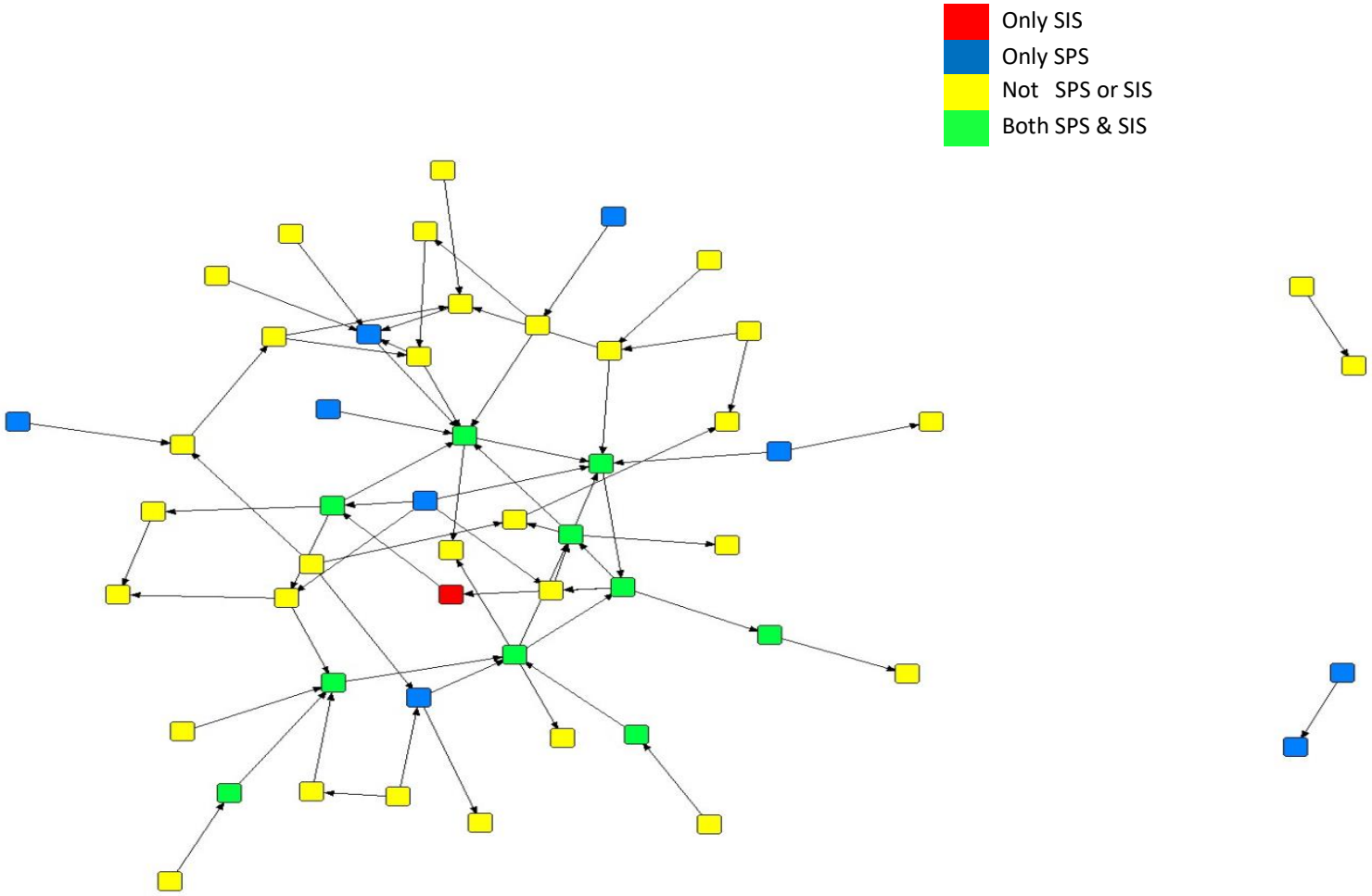

Figure 8b. Directed sociogram of preferential associations between dry-housed gestating sows for production cycle 2 (n=52). Behaviours occurred at Surgeons farm, Writtle College University, Essex between 11th December and 31st December 2017. Sociogram shows sows quantified as only socially prominent (Only SPS, n=9), only socially influential (Only SIS, n=1), both socially prominent and influential (Both SPS & SIS, n=10) or not socially prominent or influential (Not SPS or SIS, n=32).

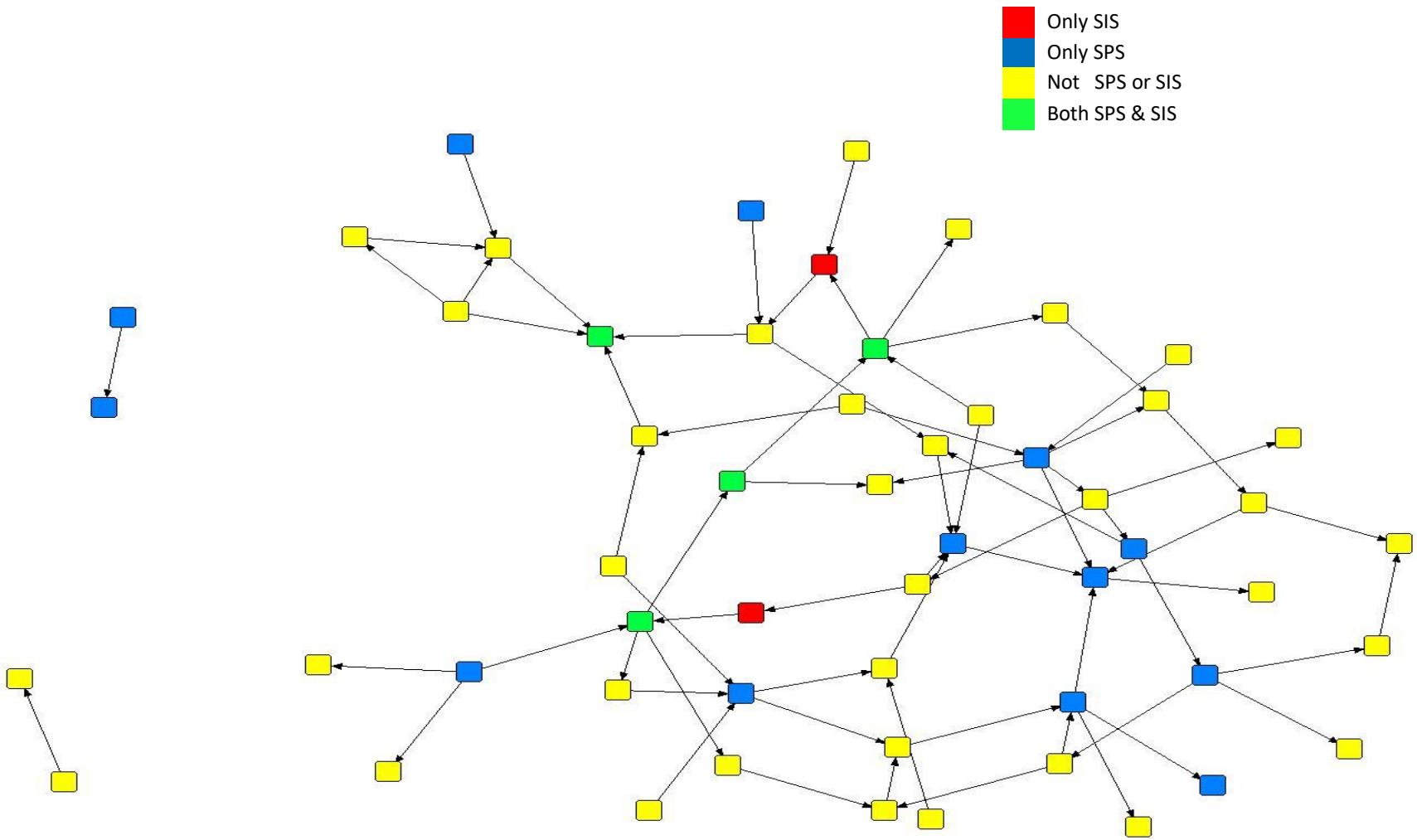

Figure 8c. Directed sociogram of preferential associations between dry-house gestating sows for production cycle 3 (n=56). Sociogram shows sows quantified as only socially prominent (Only SPS, n=13), only socially influential (Only SIS, n=2), both socially prominent and influential (Both SPS & SIS, n=4) or not socially prominent or influential (Not SPS or SIS, n=37). Behaviours occurred at Sturgeons farm, Writtle University College, Essex between 1st January and 21st January 2018.

4.3.2. Quantifying missing data

Due to the dynamic nature of the herd, sows were not consistently present during the 63 hours of observations, a result of remixing new sows or removing sows for farrowing. The data had to be weighted to account for the hours that individuals were missing from the study. In PC1, 17% of the herd (n=12) were missing from the network for 6 hours. In PC2, 23% of the population (n=12) were missing from the network for 6 hours, and 8% (n=4) were missing for 3 hours. In PC3, 21% of the herd (n=12) were absent from the network for 6 hours, with only one sow missing for 3 hours. The coefficient applied to both degree centrality, and betweenness centrality for absent sows is,

$$y = n/x.$$

Where:

y = Weighted value of interactions per hour observed

n = Value of either degree centrality or betweenness centrality

x = Number of hours observed

4.3.3. Social prominence at an individual level

Table 9. The number of individuals, not specific individuals, within each *k*-core for PC1 (n=70), PC2 (n=52) and PC3 (n=56) who quantified as socially prominent sows. These SPS had a degree centrality for preferential associations above the 95% confidence interval range for their subgroup. PC1 had a total of 21 SPS identified, which represented 30% of the network. No SPS identified in K1. The most connected subgroups (K4 & K3) contained the most prominent sows. PC2 had a total of 19 SPS identified, which represented 37% of the network. The most connected subgroups (K2) contained the most prominent sows. PC3 had a total of 17 SPS identified, which represented 30% of the network. The most connected subgroups (K2) contained the most prominent sows. The *k* values, i.e., K4, refer to the subgroup, the coreness value indicates the number of nodes an individual is connected. For example, in K3, an individual is connected to at least three other individuals and those in turn connect with at least three or more other nodes.

Production cycle and *K*-core	Degree centrality mean and standard deviation	95% Confidence Interval range	Number of socially prominent sows (SPS)
Cycle 1			
Centralisation: 0.13			
K4	20.0 ± 6.0	17.8-22.3	9
K3	10.6 ± 4.2	9.1-12.2	9
K2	7.0 ± 2.9	5.2-8.8	3
Total			**21**
Cycle 2			
Centralisation: 0.05			
K2	8.5 ± 4.2	7.0-10.0	10
K1	2.6 ± 1.2	2.1-3.0	9
Total			**19**
Cycle 3			
Centralisation: 0.07			
K2	7.9 ± 3.3	6.8-8.9	11
K1	2.5 ± 1.0	2.1-2.9	6
Total			**17**

Although there is slight variation in the total numbers of SPS in each production cycle (Table 9), proportionate to herd numbers, there are differences in the distribution of the SPS degree centrality scores for preferential associations within each network (Figure 9).

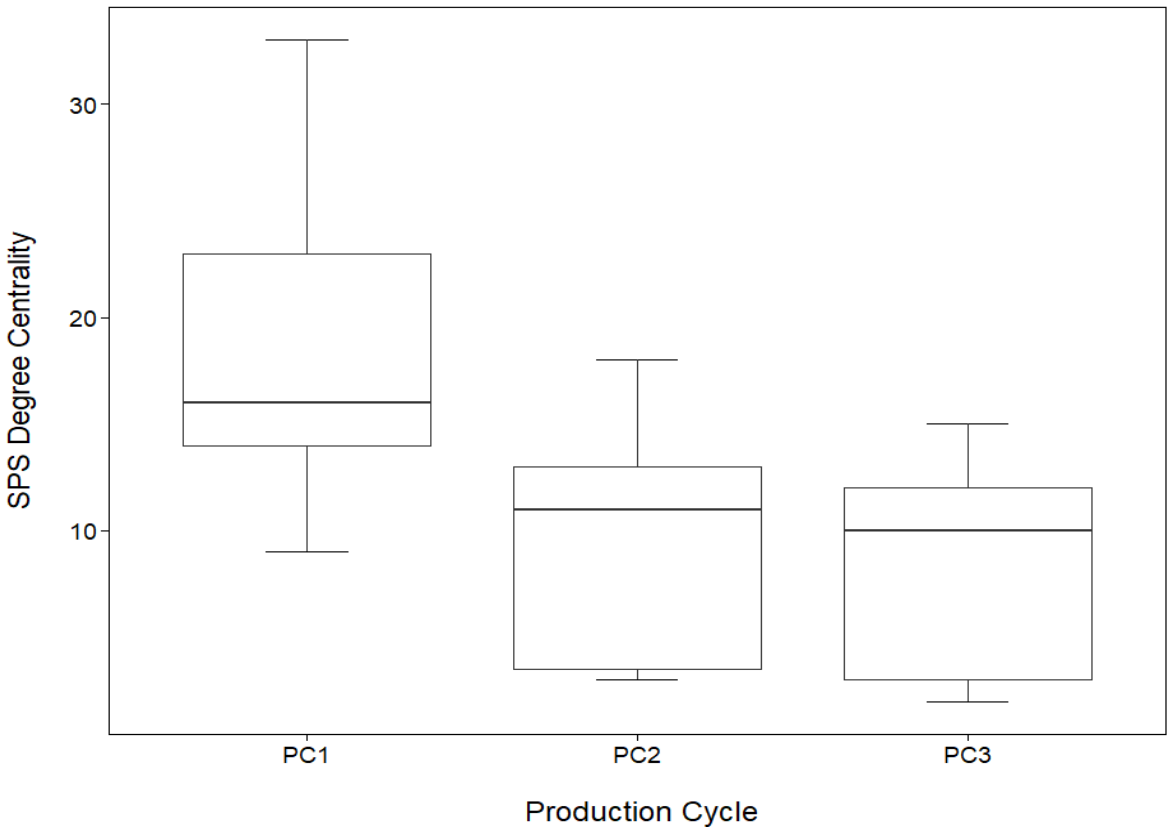

Figure 9. Degree centrality quartiles (based on preferential associations) for all three production cycles. SPS quantified in PC1 (n=21) had a median degree value of 16. 67% (n=14) of SPS in PC1 had a degree centrality above the median value. The maximum degree centrality was 33 with a minimum value of 9, giving a range of 24.SPS quantified in PC2 (n=19) had a median degree value of 11. 42% (n=8) of SPS had a degree centrality above the median. The maximum degree centrality was 18 with a minimum value of 3, giving a range of 15. SPS quantified in PC3 (n=17) had a median degree value of 10. 35% (n=6) of SPS had a degree centrality above the median. The maximum degree centrality was 15 with a minimum value of 2, giving a range of 13.

4.3.4. Social influence at an individual level

Table 10. The number of individuals, not specific individuals within each *k*-core for PC1 (n=70), PC2 (n=52) and PC3 (n=56) who quantified as socially influential sows. These SIS had a betweenness centrality for preferential associations above the 95% confidence interval range for their subgroup. PC1 had a total of 13 SIS identified, which represented 19% of the network. The most connected subgroup (K4) contained the most influential sows. PC2 had a total of 11 SIS identified, which represented 21% of the network. The most connected subgroup (K2) also contained the most influential sows. PC3 had a total of 6 SIS, representing 11% of the network. The most connected subgroup (K2) included all influential sows. The *k* values, i.e., K4 refer to the subgroup, the coreness value indicates the number of nodes an individual is connected to. For example, in K3, an individual is connected to at least three other individuals and those in turn connect with at least three or more other nodes.

Production cycle and *K*-core	Mean Betweenness centrality and standard deviation	95% Confidence interval range	Number of socially influential sows (SIS)
Cycle 1			
K4	5.9 ± 3.5	4.6-7.3	6
K3	2.8 ± 3.6	1.5-4.2	5
K2	0.7 ± 1.1	0.0-1.4	2
Total			**13**
Cycle 2			
K2	3.4 ± 4.4	1.8-5.0	8
K1	0.1 ± 0.4	0.02-0.3	3
Total			**11**
Cycle 3			
K2	2.5 ± 2.7	1.6-3.4	6
Total			**6**

Although there is slight variation in the total numbers of SIS in each production cycle (Table 10), there are differences in the distribution of the SIS betweenness centrality scores for preferential associations within each network (Figure 10).

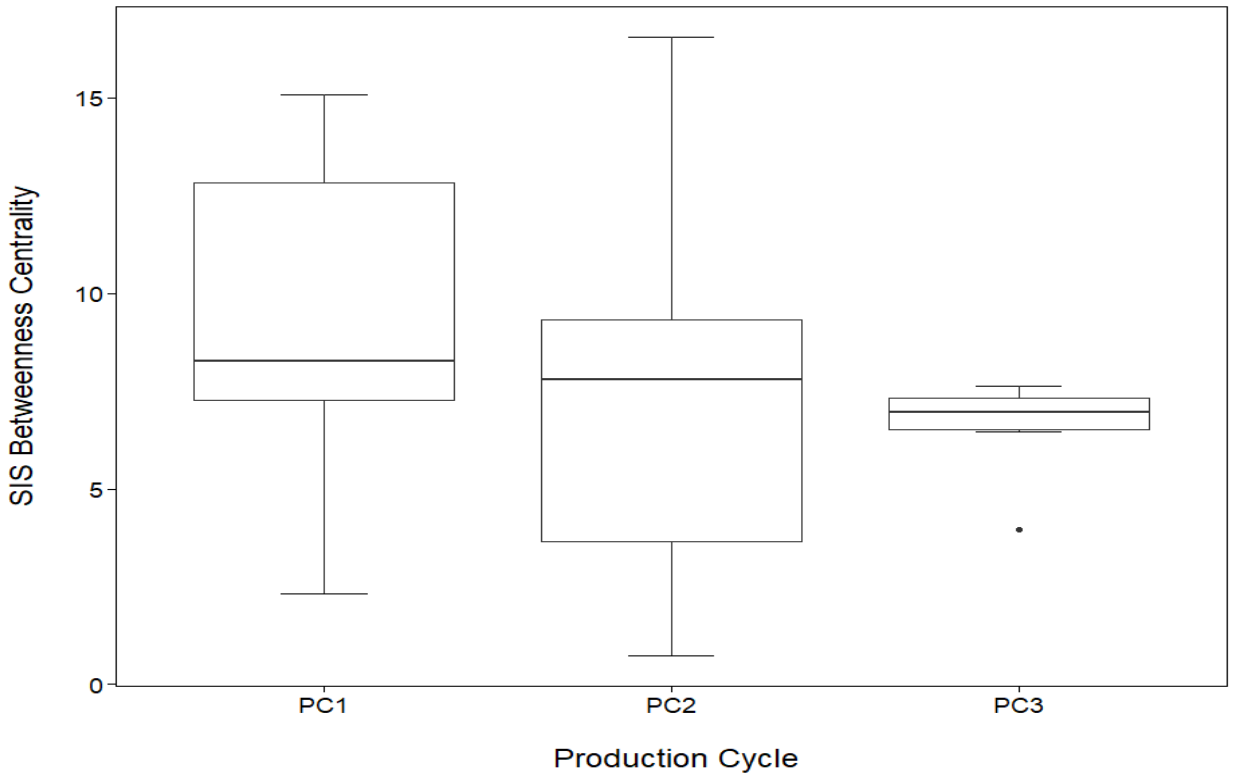

Figure 10. Betweenness centrality quartiles (based on preferential associations) for all three production cycles. SIS quantified in PC1 (n=13) had a median betweenness value of 8.3. 4% (n=6) of SIS in PC1 had a degree centrality above the median value. The maximum betweenness centrality value was 15.081, with a minimum value of 2.3, giving a range of 12.75.SIS quantified in PC2 (n=11) had a median betweenness value of 7.8. 45% (n=5) of SIS had a betweenness centrality above the median. The maximum betweenness centrality was 16.5, with a minimum value of 0.7, giving a range of 15.8. SIS quantified in PC3 (n=6) had a median betweenness value of 6.9 50% (n=3) of SIS had a betweenness centrality above the median. The maximum betweenness centrality was 7.6, with a minimum value of 3.9, giving a range of 3.7. Identified in PC3 was one outlier, with a betweenness centrality outside the 1.5* the lowest interquartile range.

4.3.5. The stability of social prominence and influence

4.3.5.1. Socially prominent sows

Within the networks, accounting for the number of times individuals were identified over the three production cycles, 27% (n=12) quantified as SPS 33% of the time, 47% (n=21) were SPS 50% of the time they were in the networks, 11% (n=5) quantified 67% of the time, and 16% (n=7) were SPS 100% of the time. Results indicate that being socially prominent was a generally transient social trait, further supported by the changes in degree centrality between production cycles. A significant decrease in degree centrality was revealed between PC1 and PC2 (coef. -0.98, z 5.703, $p < 0.001$) and between PC2 and PC3 (coef. -0.59, z -2.747, $p<0.01$). Results do not represent a deviation from chance, X2 (2, n = 178) = 0.67, $p = 0.71$.

4.3.5.2. Socially influential sows

Instability in social influence was also found, 37% (n=10) quantified as SIS 33% of the time, 48% (n=13) quantified as SIS 50% of the time, 7% (n=2) quantified 67% of the time, and 7% (n=2) were SIS 100% of the time they were in the networks. A significant decrease in betweenness centrality was revealed between PC1 and PC2 (coef. -1.48, z 3.555, $p < 0.001$) and between PC2 and PC3 (coef. -1.49, z -3.123, $p < 0.01$). Betweenness centrality is not an individually stable centrality metric overtime in the preferential association networks. Results do not represent a deviation from chance, X2 (2, n = 178) = 0.86, $p = 0.65$.

4.3.6. Network position and time spent in the herd

There were no significant differences in the betweenness centrality or degree centrality between newly remixed sows and resident pigs in all three production cycles. However, there were very highly significant differences in the degree centrality of all newly remixed sows (mean = 7.0 ± 5.9SD) compared to sows not present during the entirety of the production cycle (mean = 9.6 ± SD), coef. 0.87, z 4.689, $p < 0.001$.

4.3.7. Network position and parity

Parity was not found to be a significant predictor for degree centrality or betweenness centrality in any of the production cycles, indicating that propensity to be socially prominent or influential is not impacted upon by parity.

4.4. Discussion

Traditional methods of behavioural research demonstrate the difficulties of identifying key individuals within networks that inherently reflect a decentralised social group (Flack et al., 2005), often a result of the fission-fusion aggregations, such as those found in dynamic pig systems. The current study shows that with the application of social network analysis, identification and investigation of influential, and prominent sows can transition from the meso to the micro-level of evaluation. While additionally evaluating the rise and fall of centrality metrics in a prosocial network based upon preferential associations. The study identified socially prominent and influential sows in all three production cycles (Table 8), supporting the findings of chapter three

that all pigs are not socially equal. Results also show that although the centrality metrics for either quantified SPS or SIS did not remain stable over time, there were a small number of individuals who held the position of SPS or SIS more than once throughout the study.

The analysis of individual degree centrality and betweenness centrality discovered that numbers of socially prominent and influential sows remained consistent over all three production cycles, proportionate to the number of animals in each network (Table 9 and Table 10). The natural consistency in structure occurred despite changes in who was quantified as either SPS or SIS in each network; reflective of the maintenance in social structure expected and observed in wild boar herds. Although these positions were generally unstable (section 4.3.5.), due to the significant centrality metrics variance between production cycles, sows were shown more likely to be quantified as SPS twice than SIS as 35% of SPS held the position more than once compared to the 10% of SIS. These differences could have been contributed to by the changes in social configuration in each network (Webster and Ward, 2010) coupled with individual social discriminatory behaviour. Positive behaviour can be beneficial to the initiator and receiver (Rault, 2019). However, these associated benefits may be surpassed by more rewarding actions in response to different contexts. The low thresholds of preferential associations observed in the current study reflect that investing in another behaviour may be more worthwhile. For example, in the dynamic pig herd at Sturgeons farm investment in aggression may be more beneficial than positive behaviour. Almost certainly due to competition for valuable resources such as access to the ESF, preferred lying location, enrichment or in response to hierarchical challenges.

Individual decision-making underpins the incitement to form and maintain fission-fusion groups in wild species (Kerth, 2010). These decisions are in response to seasonal and environmental challenges such as predator avoidance (Brightsmith and Villalobos, 2011), access to resources (Lesmerises et al., 2018) or information exchange (Fishlock and Lee, 2013). Removed from commercial species is the freedom to make these group-level choices, so is the decision to form group sizes that allow for linear hierarchies and social bonds determined by familiarity, an essential component in the formation of dynamic groups (Jarman, 1974). Species innately adapted to living in much smaller, stable social groups with linear hierarchies and related conspecifics (Graves, 1984) would find this challenging in the group sizes applied to commercial farming in which large (> 50 pigs) and mega (> 100 pigs) groups are common practice (Turner and Edwards, 2004; Samarakone and Gonyou, 2008). In the current study, there are certain individual freedoms that the animals have available, such as the choice of preferred lying partner. The motivation for selecting a favoured lying partner holds confounding factors, such as do sows tolerate each other because of a preferred location in the barn or are they being socially discriminatory. There are limitations to the study in respect of this confounder, as the motivation for approaching and selecting a lying partner could not be fully differentiated between, the findings do reveal though that there is variation in social tolerance. Social tolerance is defined as a sow exhibiting tolerance towards an approaching sow in the preferential association networks when the approaching individual is neither attacked or displaced within 60s or the sow receiving the approach does not displace herself within 60s. Not all sows reacted equally to every individual that approached them, with 47% of the PC1 population demonstrating intolerance behaviour. These reactions do go some way to explaining why some sows at Sturgeons farm engage in discriminatory social behaviour and

apply different social strategies depending on the individual with whom they are interacting. It extends beyond simple tolerance because of a preferred lying location, as some sows were observed to displace themselves if an unwanted interloper approached.

The findings also show there is a greater tendency for degree centrality to be more consistent than betweenness centrality (section 4.3.5); a result also demonstrated in the hierarchical organisation of prairie dogs (Verdolin et al., 2014). Unlike the current study, the prairie dog study determined that betweenness centrality was unstable because they were observing permanent transitions of individual movement from one social group to another. Rather than a role in which the 'influential' animal was consistently moving between groups, an unsurprising result for this species as colonies will splinter if resources are limited (Travis and Slobodchikoff, 1993). In contrast, individual levels of sow centrality metrics remained significantly unstable in response to the changing social environments. In line with previous research (i.e., Formica et al., 2011), individuals are seemingly altering their behaviour in response to the social dynamics and the unpredictability of challenges that may occur, a result of different personalities within the herd (Zhu et al., 2019). In contrast, the consistency of prosocial centrality metrics is documented in other dynamic groups, including bighorn sheep, *Ovis canadenis* (Vander Wal et al., 2015), small spotted catsharks, *Scyliorhinus canicular* (Jacoby et al., 2014), eastern mosquitofish, *Gambusia holbrooki* (Flood and Wong, 2017) and Australian snubfin dolphins, *Orcaella heinsohni* (Parra et al., 2011). Most certainly, the benefits accrued through prosocial behaviours in one species may not reflect those in another.

Farine et al. (2015b) found that social gregariousness was a stable individual social metric. Their study investigated the social behaviour of blue tits, *Cyanistes caeruleus*, great tits, *Parus major*, and marsh tits, *Poecile palustris*. The research concerned the heterospecific information transference of feeding sites over three winters for the maintenance of individual and group fitness achieved through cooperative foraging and information sharing. The three bird species were shown to have a higher degree centrality when engaging with conspecifics over heterospecifics. Marsh tits were also found to be the 'keystone' animals, despite them being the least common species. Marsh tits were significantly more prominent intra-flock, enabling information to diffuse more effectively with their conspecifics and additionally demonstrated asocial behaviour for finding new feeding sites. Farine et al., (2015b) cited that identifying these influential individuals is essential as '*they determine where the information is 'seeded' in the group and the subsequent pathway of diffusion'*. By contrast, Jacoby et al. (2014) revealed social relationships between juvenile sharks that aggregated, showing associated benefits for reducing predation. Nonetheless, these social interactions decreased when the sharks entered an environment that provided more effective camouflage and therefore became less dependent on their conspecifics for anti-predator strategies. Likewise, in the current study, these findings show that individuals exhibit plasticity in social activities in response to a changing environment by altering their behavioural interactions and giving rise to the instability of centrality metrics. Context of behaviour is, therefore, an essential element for the individual level decision to initiate changes in response to the environmental factors described. Where there is value in positive behaviour, such as cooperation for survival, it is clear to see why some species engage in prosocial behaviour, albeit temporarily in some cases. In contrast, commercial animals may not be as highly

motivated to invest in affiliation within environments where 'working together' or forming social bonds have costs that outweigh the benefits. A lack of reciprocation of preferential associations between socially preferred pigs and those that were not as 'popular' highlighted this in chapter three.

The formation of affiliative bonds may also be impacted upon by intrinsic factors, a longitudinal study of bighorn sheep (Vander Wal et al., 2015) found that although social centrality remained consistent, the metric was impacted upon by the reproductive state. It is not surprising that behaviour states may alter during gestation, with endocrine changes serving to facilitate parturition and lactation, affecting cognitive processes (Russell et al., 2001). Stage of gestation, when housed in the dry barn, could be a confounding factor that affects the centrality metrics of the preferential associations shown in the current study, particularly as social prominence and influence is not impacted upon by parity. As such, experience and body size did not affect affiliative behaviour in the dynamic herd, a result consistent with previous research in both pigs and other species (Durrell et al., 2004; Verdolin et al., 2014). There were no significant differences between the overall degree centrality or betweenness centrality of newly introduced sows and resident sows over the three-week production cycles, despite new sows demonstrating significantly lower degree centrality than sows that were due to farrow. These findings do not appear to be consistent with other research; differences in methodology may be the key. For example, Krauss and Hoy (2011) found that newly remixed sows demonstrated significantly higher levels of discriminatory lying events within the first 24 hours after remixing than resident sows. Discrimination was revealed by interactions occurring within a subgroup (i.e., resident, or new

sow). However, unlike the current analysis that took an overall measure of centrality metrics for individuals within a production cycle, Krauss and Hoy examined daily changes in behaviour. They found that although newly remixed sows initially engaged in higher affiliative behaviours than resident sows, these differences were no longer significant after three weeks. These inconsistencies demonstrate that the timing of observations of newly remixed sows is key to obtaining a true reflection of behaviour changes.

Despite the lack of meaningful centrality differences between new sows' and resident pigs (section 4.3.6.), degree centrality revealed significantly lower results for recently inseminated sows' relative to sows that were due to farrow. The analysis between resident sows and newly mixed sows did not distinguish between coreness value but rather the levels of centrality metrics and therefore does not promote that high centrality metrics indicates high discrimination, as interactions may have been directed at multiple individuals rather than a select few. However, it is suggesting that sows that have been in the network longer are more inclined to engage in behaviour that is socially more readily discriminatory. A lack of social prominence and influence with new sows in the preferential association networks resulted in the small percentage of new sows quantified as SPS and SIS compared to resident sows. Social integration may be a factor contributing to the differences in the network positions of newly remixed sows' relative to resident sows. However, the gestation state also affects centrality metrics, as shown in the bighorn study (Vander Wal et al., 2015), indicating that stage of gestation could be an influencing parameter in prosocial behaviour. Progesterone regulates the development of embryos during early pregnancy by thickening the walls of the uterus, facilitating a reduction in prepartum losses in mammals (Ye et

al., 2019). Research has documented a negative correlation between levels of aggression and progesterone (Fraile et al., 1987; Kohlert and Meisel, 2001). During pig reproductive processes, levels of progesterone plateau 16 days after insemination and remain stable until parturition (Cole and Cupps, 1977). Mixing sows at a later stage of pregnancy has been shown to reduce aggression as the social hierarchy stabilises (Stevens et al., 2015). During the present study, sows were remixed within approximately 2-3 days after insemination. It is indicating that newly remixed sows are less prominent and influential in the preferential association networks potentially due to their propensity for higher aggressiveness than sows further along in their stage of pregnancy. A later chapter will investigate the relationship between prominence, influence, and aggression.

The majority of SPS and SIS in all three networks demonstrated a higher rate of connectivity with their conspecifics, as reflected in their coreness value (Table 9 and Table 10). Gonyou (2001) proposes that within large commercial herds, as social hierarchy becomes decentralised, smaller subgroups will form. By evaluating the *k*-cores in addition to centrality metrics, this novel approach shows the value of applying the coefficient that quantifies SPS and SIS to the whole network. Without consideration of the potential subgroups, prominent and influential sows, that are engaging at a lower threshold of connectedness, would not be identified; shown as SPS, and SIS quantified in the lowest and highest connected subgroups. So, prominence and influence are not shown to be attributes specific to those individuals who are in the most highly connected and cohesive subgroups. It could be argued that defining influential and prominent sows at the *k*-core level rather than at the pen level over-estimates the true number of keystone individuals within the herd. However, the findings showed assortment by subgroup and as an overview of behaviour,

this demonstrates that all individuals have the potential to impart effect, even at a localised level regardless of social standing. Concerning the transmission of behaviour, disease, or information this is particularly relevant to welfare and health. For example, in rhesus macaques (*Macaca mulatta*), while individuals at the top of the social hierarchy are more prominent in terms of transmission, lower-ranking individuals (the groomers) are more influential with the greater capacity to transmit parasites or disease (Balasubramaniam et al., 2019). This strategy is further documented in Hawaiian monk seals (*Monachus schauinslandi*), in which the vaccination of less prominent individuals is still an effective mechanism for whole population health (Robinson et al., 2018). If the current study had only considered sows at the top of the social hierarchy it would have discounted the impact that every individual is potentially capable of and not have been a true reflection of the complexities of the social interactions within the dynamic herd, particularly due to the behavioural instability. The rationale for the selection of *k*-cores may have been further supported with the implementation of eigenvector centrality, a measure of the number and quality of a node's social partners (Brent, 2015). Borgatti et al., 2018 describes eigenvector centrality as '*as a measure of popularity, where a node with high eigenvector centrality is connected to nodes that are themselves well connected*'. Although, in the current study, individuals were not restricted to interactions with members of an alternative *k*-core, the application of eigenvector centrality may have provided an alternative perspective of potential social selections to extend upon the centrality metrics used (Foister et al., 2018). The distribution of potentially significant individuals throughout the herd at Sturgeons farm provides an alternative perspective, converse to traditional measures of prominence such as aggression (Arey and Edwards, 1998). Notable animals are typically deemed to be individuals with high-ranking

positions, established through fighting (Holekamp and Strauss, 2016). The results also demonstrate that perceived dominance and prosocial prominence, and influence are not synonymous.

When evaluating the results of this research, the role of personality in the context of sociability must also be considered as stability of character is pivotal for making predictions of future behaviour across contexts. Variation in individual centrality metrics over time and set in the current study suggests that social prominence and influence, based upon preferred lying behaviour or affiliation, may not serve as a compelling predictive aspect of personality in dynamic pig herds. Unlike other species, the stability of individual sociability and affiliative behaviour across time and settings is documented in wild social groups, including chacma baboons, *Papio hamadryas ursinus* (Castles et al., 2014), ring-tailed lemurs, *Lemur catta* (Kulahci et al., 2018a) and guppies, *Poecilia reticulata* (Krause et al., 2017). Nevertheless, while sociability in pigs is considered one of the five main personality traits (Finkemeier et al., 2018), the stability of affiliative behaviours in pigs over time and context is not well documented (O'Malley et al., 2019). Research by Foris et al. (2018) may go some way to explain and support the findings of the current study. Investigation of the temporal and situational consistency of personality traits in dairy cows found that while the characteristics of activity and boldness were stable in individual tests, at a group level, when the social network became unstable, individuals altered their levels of behaviour. The study concluded that the personalities comprising a social group have a significant impact on how an individual will react to its conspecifics and environment. Like dairy cattle, the sows at Sturgeons farm demonstrate unstable centrality metrics because they are responding to

the personality changes in the herd. Thus, suggesting that individual personality testing would not be a useful measure of predictive personality at group level in a dynamic commercial system.

Consistency in centrality metrics, based upon prosocial behaviour is, therefore, pivotal for predicting future responses, allowing for the application of effective management strategies. Central individuals can positively encourage group fitness to enhance benefits through socially influential expressions. Non-aggressive and prosocial behaviour is one mechanism where stable network positioning and social role reduces agonistic interactions by maintaining group cohesion. These behavioural mechanisms are reported in both wild and commercial species (Lusseau and Newman, 2004; Flack et al., 2005; Kanngiesser et al., 2011; Šárová et al., 2016), with the removal of critical individuals increasing aggression and destabilising the social group (Tokuda and Jensen, 1968; Beisner et al., 2019). Robust social networks, in which individuals consistently maintain their network position, allows for more predictive measures of potential intervention. Despite this, although the current study found that individual centrality metrics were not stable and subsequently not predictable over the production cycles, it does provide valuable insight in revealing that there are prominent and influential individuals within the prosocial networks.

Centrality and prominence are, however, a double-edged sword, these individuals can have increased fitness (McDonald, 2007) and survival (Silk et al., 2003) but are also at higher risk of disease and parasites (Silk et al., 2016). Therefore, regardless of centrality metric instability at an individual level, understanding that there are prominent and influential sows, consistent at a group level, in a decentralised dynamic herd is critical. Further, indicating a path forward for

enhancing welfare through early detection of disease and intervention. As a welfare indicator, this gives support to the use of directed and weighted networks over binary networks, as the level of intensity of interactions and direction is an essential factor for assessing the potential for transmission of disease or parasites (Chen and Lanzas, 2016). The use of both degree centrality and betweenness centrality is also supported when considering how pathogens could be transmitted through the herd as prominent individuals are not necessarily influential individuals, as shown in the current study. The more interactions there are between individuals (i.e., degree centrality), the higher the risk of any potential transmission. Individuals with high betweenness centrality (i.e., SIS) have a more significant potential to transmit disease outlined in the susceptible-infected-susceptible compartment modelling framework for pathogen transmission (Chen and Lanzas, 2016). This model demonstrates how infected nodes can spread illness to susceptible nodes, but that contact between vulnerable nodes does not transmit pathogens. As such, nodes with higher betweenness centrality can infect individuals more rapidly because they are sitting on the most geodesic paths in a network.

Identifying all potential prominent and influential individuals, regardless of their overall connectedness, would be an essential component when implementing preventative health measures. For example, for conservation purposes whole-population vaccinations are incredibly challenging and wild species research documents the value of identifying key individuals for preventative health measures. Robinson et al. (2018) found that vaccinating key spreaders against the significant threat of morbillivirus in a population of endangered Hawaiian monk seal is an effective mechanism for whole group immunisation. While Balasubramaniam et al., (2019)

identified that the most central individuals in the grooming and huddling network of rhesus macaques, *Macaca mulatta*, were also most pivotal in the *Escherichia coli* transmission network. This research direction lends support that by utilising this method of preventative veterinary medicine (i.e., identify the super-spreaders) could be adapted to health management in commercial herds. British pigs are currently at risk of African swine fever and Porcine epidemic diarrhoea virus (AHDB, 2019) while continuing to be at risk from Foot and Mouth disease and Classical swine fever. Extensive research has focused on the identification of prominently aggressive individuals aiming to address the long-standing welfare and production concerns associated with large-scale commercial housing (Hoy et al., 2009a; Verdon et al., 2018). By contrast, there is a small body of work (i.e., Durrell et al., 2004; Rault, 2012; Abeyesinghe et al., 2013; Reimert et al., 2014; Rault, 2018) that is moving towards addressing such commercial farming issues from the perspective of prosocial behaviours and affiliative bonds. Thus, providing a platform for investigating the effects on welfare and production, through the identification of those that are engaging in prosocial behaviours promoting an alternative approach to pig management strategies. Chapter five will investigate the effect of preferential association centrality metrics on productivity and maternal behaviour.

4.5. Conclusions

Through the application of social network analysis, this study has identified socially prominent and influential individuals, despite overall social decentralisation in all three production cycles, supporting the findings of chapter three that all pigs are not socially equal. The instability of

individual centrality metrics, based upon preferential associations, highlights the complexities involved in predicting levels of prosocial activities in a dynamic pig herd. It is an important finding, because predictive management and intervention strategies at an individual level may become challenging due to only a small number of individuals shown to be either SPS or SIS more than once. The social inequality demonstrates that there are individuals in the herd who could potentially be 'super-spreaders' or indicators of the general health of the herd. The critical evaluation also reveals that consideration of reproductive state and stage of gestation is crucial when evaluating findings in future related studies, as they can impact the motivation to engage in affiliative behaviours. The results suggest that prominence and influence are unstable because they are affected by the social context. In response to environmental changes and social dynamics, flexible individual behavioural strategies determine degree and betweenness centrality. Other characteristics such as morphological factors including parity, body size and subsequent experience are not shown to be pivotal in being able to predict if an individual is more likely to be socially prominent or influential. It is context-dependent decision-making at an individual-level that determines the behavioural strategies employed, based upon preferential associations, in a dynamic breeding sow herd.

Chapter Five:

The impact of social prominence and influence in three preferential association networks on reproductive performance

5.1. Introduction

Deleterious effects of undesirable behaviours, brought about by intensive and dynamic farming, are extensively documented (von Borell, 1995; Rodenbury and Koene, 2007; Peden et al., 2018). Research has predominantly focussed on seeking strategies to reduce these behaviours in numerous species including cattle, pigs, and chickens (Jensen, 2018; Peden et al., 2018; Zepp et al., 2018). By comparison, the impact of management strategies that could improve welfare and production, which are determined by our understanding of socio-positive interactions has received little attention. Prosocial behaviours fall into numerous categories including, caregiving, affiliation, sharing, social teaching and cooperation (Rault, 2019). The benefits of prosocial behaviours, at both the individual and group level, may arise from the likelihood of reciprocation or the inclusive fitness of cooperative behaviour. As such, from a socio-biological perspective, all prosocial behaviours will enhance indirect long-term group benefits; as intrinsically linked with welfare are fertility and reproduction (Pizzari, 2016). Numerous wild species studies have documented the relationship between prosocial behaviours and reproductive success. An increased number of social bonds can enhance offspring production (Schülke et al., 2010), improve reproductive success (Ramp et al., 2010; Kohn, 2017) and strengthen offspring survival in a range of species (Silk et al., 2003; Cameron et al., 2009; Silk et al., 2009). There is currently little understanding of the association between prosocial behaviours and reproductive performance in commercial animals (Rault, 2012).

The transition to welfare and production enhancing strategies founded in socio-positive

interactions must employ an approach capable of identifying behaviours at a group and individual level. Social network analysis (SNA) enables such an in-depth investigation, by identifying animals in network positions who can potentially feature as important assets in achieving enhanced welfare. For example, McFarland et al. (2015) demonstrated that vervet monkeys with the highest rates of social connections achieved more thermal benefits than those who had fewer social contacts. Although the direct benefits of increased prosocial interactions may seem obvious, with indirect benefits, not enough knowledge is known. Benefits arising from indirect interactions that improve reproduction may potentially serve as a mechanism for promoting social stability and subsequently decreasing aggression. In rhesus macaques, research has documented that in addition to the fitness enhancing effects of direct grooming, indirect grooming, measured by proximity to those who groomed also improved reproductive success (Brent et al., 2013). The study also revealed that the characteristics of the initiators and recipients of indirect interactions impacted offspring survival. Aggressive macaques who frequently associated with other aggressive macaques had increased offspring survival, as did passive macaques that regularly associated with other passive macaques. Indicating a complex social strategy of the selective association through indirect interactions to improve fitness and reproduction at both an individual and group level.

Preweaning piglet mortality and fetal deaths constitute the greatest threats to economic losses and present ethical challenges (Kilbride et al., 2014; Muns et al., 2016). Crushing and starvation are the significant contributors to all postpartum deaths (Dyck and Swierstra, 1987; Marchant et al., 2000; Jarvis et al., 2005), accounting for 70%-80% of mortality (English and Morrison, 1987).

Also, stillbirths and foetal mummification contribute to approximately 4-8% of pre-parturition losses (English and Morrison, 1987). Additionally, with increased tensions and agonistic interactions resulting from the introduction of group housing, an association has been made between social stress during gestation and latency to respond in piglet distress tests (Ringgenberg et al., 2012), a promoting factor towards fatal crushing events. Stressors during pregnancy have highlighted the detrimental effect on piglet development and survival rates (Tuchscherer et al., 2002; Kranendonk et al., 2006a.; Kranendonk et al., 2006b). Research has extensively focussed on the impact of agonistic behaviours, intending to improve reproductive performance. The suggestion of an association between prosocial behaviours and enhanced reproduction in other species presents an alternate perspective from which to develop an innovative approach that informs management procedures in commercial pigs. The application of SNA will provide a unique technique of how socio-positive interactions may affect productivity and maternal behaviour in breeding sows. The aim of this study then is to investigate the relationship between being either socially prominent or influential, based upon preferential associations, and reproductive performance by analysing the effect of these social roles on prepartum piglet mortality, pre-weaning piglet mortality and maternal behaviour. The research will evaluate the inter and intra-individual variation in production metrics across three production cycles and assess the effect of parity on these measures.

5.2. Methods

Chapter two provides a detailed description of the methods. A summary is outlined in the following sections:

5.2.1. Animals and housing

The study was conducted at Sturgeons farm, Writtle University College, Chelmsford, Essex between November 2017, and January 2018. The study group consisted of a commercial cross of Large White-Landrace and Pietrain breeds; parities one to seven, housed in a dry sow barn. Sows were fed on a complete feed for breeding sows through electronic sow feeders, reset daily at 15:00 h, with additional access to *ad libitum* straw. Sturgeons farm operates a dynamic system in which small groups of sows are remixed into the herd every third Tuesday. There is a repeated cycle of production following the pattern, farrowing week, breeding week, and weaning week. For individual identification, each sow was marked with coloured dots, stripes, or both on their backs. Colour codes corresponded to ear-tag number.

5.2.2. Data collection

5.2.2.1. Sow reproductive data

Access to the farm diaries and liaising with the pig unit manager provided relevant information concerning parity, farrowing date, insemination date and date of remixing. Diaries also provided all data concerning reproduction, including, live-born piglets, stillborn piglets, mummified foetuses, and any cause of piglet mortality following birth until weaning, including, hypothermia,

starvation, scours, crushing, lameness, low viability, and unknown causes of preweaning death. Data was taken from the farrowing event that occurred directly after a sow had been removed from any of the three production cycles to investigate associations between production and social network metrics. Data was also taken for the farrowing event that followed the first to investigate the stability of reproductive performance. Data for the second farrowing event was not available for every sow observed during the three production cycles due to culling or a second farrowing event had yet to occur before analysis. Table 11 provides a detailed description of the production metrics.

Table 11. Categories and definitions of piglet mortality.

Categories of piglet mortality	Definition of category
Prenatal mortality	
Stillborn piglets	A piglet that died shortly before or during parturition with no sign of decay (Vanderhaeghe et al., 2013).
Mummified foetus	Death during gestation with signs of mummification (Pandolfi et al., 2017).
Postpartum mortality	
Low-viability piglet	Death due to low vigour or physical strength (Muns et al., 2016).
Starvation	Death occurring when the piglet is emaciated (Westin et al., 2015).
Hypothermia	Death due to low ambient body temperature with the inability to maintain thermoregulation (Berthon et al., 1994).
Scours	Death due to diarrhoea (Nabuurs et al., 1993).
Lameness	Abnormal gait (Meijer et al., 2015) resulting in euthanasia.
Crushing	Death due to crushing or smothering by the sow (Galiot et al., 2018).
Unknown	Any unknown cause of death.

5.2.2.2. Video observation data

A total of five CCTV H.265 4Mega Pixel Eyeball PoE, infrared Dome cameras were installed in the dry barn to capture and observe sow behaviour. Each camera was positioned to provide unobstructed, direct visual access to all essential functional areas (Chapter two, Figure 3). The areas included the straw bedded area, the passageway, the isolation pen, the ESF area and the nipple-drinkers. Three hours per day were selected for observation, 08:00-09:00 h, 15:00-16:00 h and 20:00-21:00 h. Observations occurred over three 21-day production cycles from 20th November 2017 to 21st January 2018. The video observations occurred on seven preselected days of each production cycle, including the day before remixing (day 20) and the day of mixing (day

21). The observations continued, on the three consecutive days following a mixing event (days 1,2,3). Days 7 and 14, following remixing, were also selected. Hereafter production cycle one, production cycle two and production cycle three will be referred to as PC1, PC2 and PC3, respectively. Overall, the study included 21 h of video footage for each production cycle providing 63 h of behaviours for analysis.

5.2.2.3. Social behaviours

All occurrences of preferential associations (Chapter three, Table 4) in PC1, PC2 and PC3 were captured using video observations during the predetermined periods. Preferential associations were observed to establish the presence of social discrimination. The social selections of resting partners were determined by recording who approached whom to rest with over time and if these approaches were tolerated and reciprocated. The initiator and receiver of each behaviour were recorded to enable directional ties to be identified during the analysis. Threshold measures were applied to each network to account for a preferential association rather than a random interaction, with the mean number of prosocial advances calculated for the 21 hours of observations in each production cycle**.** For all production cycles, the threshold measure was inclusive of ≥ 2 preferential interactions between an initiator and the same recipient.

5.2.3. Network construction

5.2.3.1. Identification of subgroups

K-cores have been applied to each preferential association network in the production cycles to ascertain subgroups based upon connectedness. A *k*-core is a subgraph in which every node has

degree *k* or more connections with other nodes within the subgraph (Borgatti et al., 2018). For example, in a 3-core subgraph, nodes will be connected to at least three other nodes, which in turn connect with at least three or more other nodes. The *k*-core reflects the number of individuals whom a sow connects with; it does not show the frequency of interactions.

5.2.3.2. Quantifying social prominence in the preferential association networks

Socially prominent sows (SPS) are individuals who have significantly higher overall levels of preferential associations than their *k*-core conspecifics. To calculate all interactions, indegree and outdegree will be combined for analysis. Within the preferential association networks in all three production cycles, SPS will be defined as an individual with a degree centrality above the 95% confidence interval of the degree centralities of the *k*-core population (adapted from Verdolin et al., 2014). Hereafter, socially prominent sows will be referred to as SPS and a sow not quantified as SPS will be referred to as non-SPS.

5.2.3.3. Quantifying social influence in the preferential association networks

Individuals identified with a significantly higher betweenness centrality than their *k*-core conspecifics are referred to as socially influential sows (SIS). Within the preferential association networks in all three production cycles, SIS will be defined as any individual with a betweenness centrality above the 95% confidence interval of the betweenness centralities of the *k*-core population (adapted from Verdolin et al., 2014). Hereafter, socially influential sows will be referred to as SIS and a sow not quantified as SIS will be referred to as non-SIS.

5.2.3.4. The coefficient for quantifying SPS and SIS in preferential association networks

Socially prominent and influential sows either identified as those individuals whose degree centrality or betweenness centrality or both fell above the 95% confidence interval range for their assigned subgroup (*k*-core). This method is consistent with previous social network research (i.e., Verdolin et al., 2014). These individuals quantified applying the following coefficient, $x \pm z * s/ \sqrt{n}$. Where:

x = Mean degree centrality or the betweenness centrality for the *k*-core

z = 1.96, for the 95% confidence interval

s = Standard deviation of the degree centrality or the betweenness centrality for the *k*-core

$\sqrt{n}$ = Square root of the *k*-core population total

5.2.4. Data analysis

Matrices of the preferential association networks for each production cycle were constructed in Excel and imported into Ucinet 6, version 6.634 (Borgatti et al., 2002). The general network and individual network metrics analysed in Ucinet included degree centrality and betweenness centrality. Statistical analysis was performed in R.3.4.1 (R Development Core Team, 2017). Data were subsequently tested for normality via histograms and the Shapiro Wilks test. The data were found to be nonnormally distributed. GLMMs were performed in R.3.4.1 (R Development Core Team, 2017) using the R package lme4, version 1.1-21 (Bates et al., 2015) to test for differences in production metrics between quantified and non-quantified sows. The multiple GLMMs were corrected to reduce the risk of type 1 errors with the application of the false discovery rate (FDR). Additional testing was also conducted to investigate differences in production metrics over two

farrowing events. Upon testing, the negative binomial model was found to be the best fit for the probability distribution. For each model, the pig identification number represented the random effects, and fixed effects included farrowing event and social role. Associations between the centrality metrics (degree centrality and betweenness centrality) and production metrics were performed using the Spearman's rank correlation coefficient using the R package corrplot, version 0.84 (Wei and Simko, 2017).

5.3. Results

5.3.1. The identification of socially prominent sows

Please refer to Table 9 in Chapter four that provides a detailed description of the socially prominent sows (based upon preferential associations) identified within the subgroups of PC1, PC2 and PC3. PC1 quantified 21 SPS, PC2 quantified 19 SPS and PC3 quantified 17 SPS. Table 9 shows the number of individuals, not specific individuals. Degree centrality data is weighted to account for times when sows were absent from a network.

5.3.2. Production metrics and social prominence

Table 12. The mean frequency ± SD for live-born, prenatal and postpartum piglet mortality rates for SPS and Non-SPS in PC1 (n=70), PC2 (n=52) and PC3 (n=56). [α]There were close to significant differences in stillbirths between SPS and Non-SPS in PC1 (p=0.08) and PC2 (p=0.08). Significant differences in crushing behaviour revealed in PC1 (p=0.05). PC = Production cycle. SPS = Socially prominent sow. Non-SPS = sow not quantified as socially prominent. SD = Standard deviation.

Production metric	PC1 (n=70) Mean frequency ± SD	PC2 (n=52) Mean frequency ± SD	PC3 (n=56) Mean frequency ± SD
Live-born	SPS: 12.0 ± 4.2 Non-SPS: 12.3 ± 3.5	SPS: 13.1 ± 2.7 Non-SPS: 12.5 ± 3.8	SPS: 13.4 ± 3.9 Non-SPS: 12.7 ± 3.0
Stillborn	SPS: 1.3 ± 3.3[α] Non-SPS: 1.9 ± 2.6[α]	SPS: 0.9 ± 1.6[α] Non-SPS: 2.1 ± 2.9[α]	SPS: 1.3 ± 1.6 Non-SPS: 2.3 ± 3.6
Mummified foetuses	SPS: 0.3 ± 0.8 Non-SPS: 0.2 ± 0.5	SPS: 0.3 ± 0.7 Non-SPS: 0.1 ± 0.3	SPS: 0.2 ± 0.5 Non-SPS: 0.13 ± 0.4
Total prenatal mortality	SPS: 1.6 ± 3.4 Non-SPS: 2.1 ± 2.8	SPS: 1.2 ± 1.8 Non-SPS: 2.2 ± 3	SPS: 1.5 ± 1.7 Non-SPS: 2.4 ± 3.7
Low viability	SPS: 1.0 ± 1.5 Non-SPS: 0.6 ± 1.1	SPS: 0.8 ± 1.1 Non-SPS: 1.0 ± 1.5	SPS: 1.1 ± 1.5 Non-SPS: 0.9 ± 1.5
Crushed	SPS: 1.0 ± 1.2[α] Non-SPS: 0.4 ± 0.9[α]	SPS: 0.4 ± 0.7 Non-SPS: 0.8 ± 1.2	SPS: 0.5 ± 0.9 Non-SPS: 0.5 ± 1.0
Total postpartum mortality	SPS: 2.6 ± 2.7 Non-SPS: 1.9 ± 2.1	SPS: 2.0 ± 2.1 Non-SPS: 2.2 ± 2.6	SPS: 2.4 ± 2.3 Non-SPS: 1.5 ± 2
Total piglet mortality	SPS: 3.7 ± 3.8 Non-SPS: 4.1 ± 3.3	SPS: 3.2 ± 3.1 Non-SPS: 4.5 ± 3.5	SPS: 3.8 ± 2.7 Non-SPS: 4.0 ± 4.0

5.3.3. The relationship between degree centrality and production metrics

The network centrality metrics of all three production cycles were combined to investigate an overall association between degree centrality and reproductive performance. Associations do not account for whether an individual is quantified SPS, instead refers only to the degree centrality data. This combined approach was taken due to the instability of social roles between cycles, as such individuals may have altered their behaviour patterns in response to changes in the social

configuration promoting a change in degree centrality at an individual level. Therefore, associations include every individual in all three production cycles, where production data was available (n=178). Associations were found between degree centrality and stillborn piglets (Figure 11) and, between degree centrality and crushed piglets (Figure 12).

5.3.3.1. Degree centrality and live-born piglets

No association was found between degree centrality and production rate, r_s = -0.097, p = 0.2. Live-born numbers remained consistent over all three networks for both SPS and non-SPS with no significant effect of social role on live-born numbers (Table 12). Furthermore, there were no significant differences in litter size between SPS and non-SPS.

5.3.3.2. Degree centrality and prenatal piglet mortality

No association was found between degree centrality and the rates of mummified piglets (r_s = 0.024, p = 0.75). Also, at an individual level, there were no significant differences in the numbers of mummified foetuses and network position, coef. 0.006, z 0.013, p = 0.99. There was a weak negative association between the degree centrality of the sows observed in all three production cycles and stillbirths, which was statistically significant, r_s = -0.17, p = 0.03 (Figure 11).

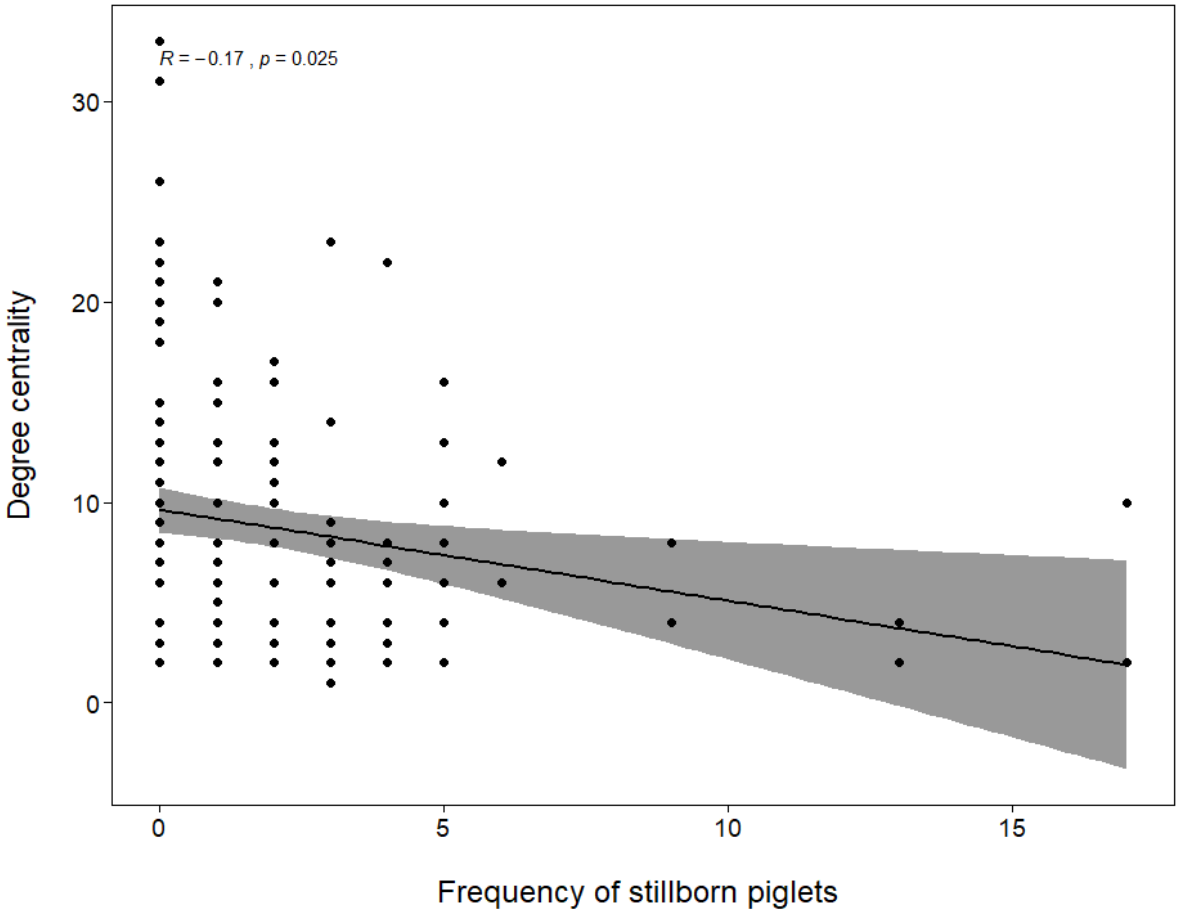

Figure 11. A weak, negative association occurred between the degree centrality and the frequency of stillborn piglets using the data from all sows in the three production cycles (n=178). The association was significant. Degree centrality refers to the total number of initiated and received preferential associations.

The impact of being socially prominent on stillbirths presented in all three networks, SPS consistently demonstrated lower rates of stillbirths than non-SPS in all production cycles (Table 11). There was a tendency towards $p = 0.05$ in two of the networks; in PC1, coef. -0.84, z -1.746, $p = 0.08$, SPS had a lower rate of stillbirths (1.3 ± 3.3SD) compared to non-SPS (1.9 ± 2.6SD). In PC2, coef. -0.83, z -1.771, $p = 0.08$, SPS (0.9 ± 1.6SD) also had a difference close to significance compared to non-SPS (2.1 ± 2.9SD). All sows were categorised as a sow with stillborn or without to investigate further the effect of preferential associations on stillbirths. Sows with stillborn were

revealed to have a significantly lower degree centrality than sows without stillborn piglets (coef. -0.27, z -2.534, $p < 0.05$).

5.3.3.3. Degree centrality and postpartum piglet mortality

No association was found between degree centrality and low viability piglets or between degree centrality, and other postpartum mortality resulting from causes including lameness, hypothermia, scours, starvation, or unknown reasons. There was a weak positive association found between degree centrality and crushing behaviour over all three networks (n=178), which was statistically significant, $r_s = 0.19$, $p = 0.012$ (Figure 12).

At an individual level, there were only significant differences in crushing behaviour between SPS and non-SPS in production cycle 1 (Table 12). Sows in all three production cycles were categorised as a sow that crushed or a non-crushing sow to investigate further the effect of preferential associations on crushing behaviour. Sows with crushed piglets were revealed to have a significantly higher degree centrality than sows with no crushed piglets (coef. 0.27, z -2.389, $p < 0.05$).

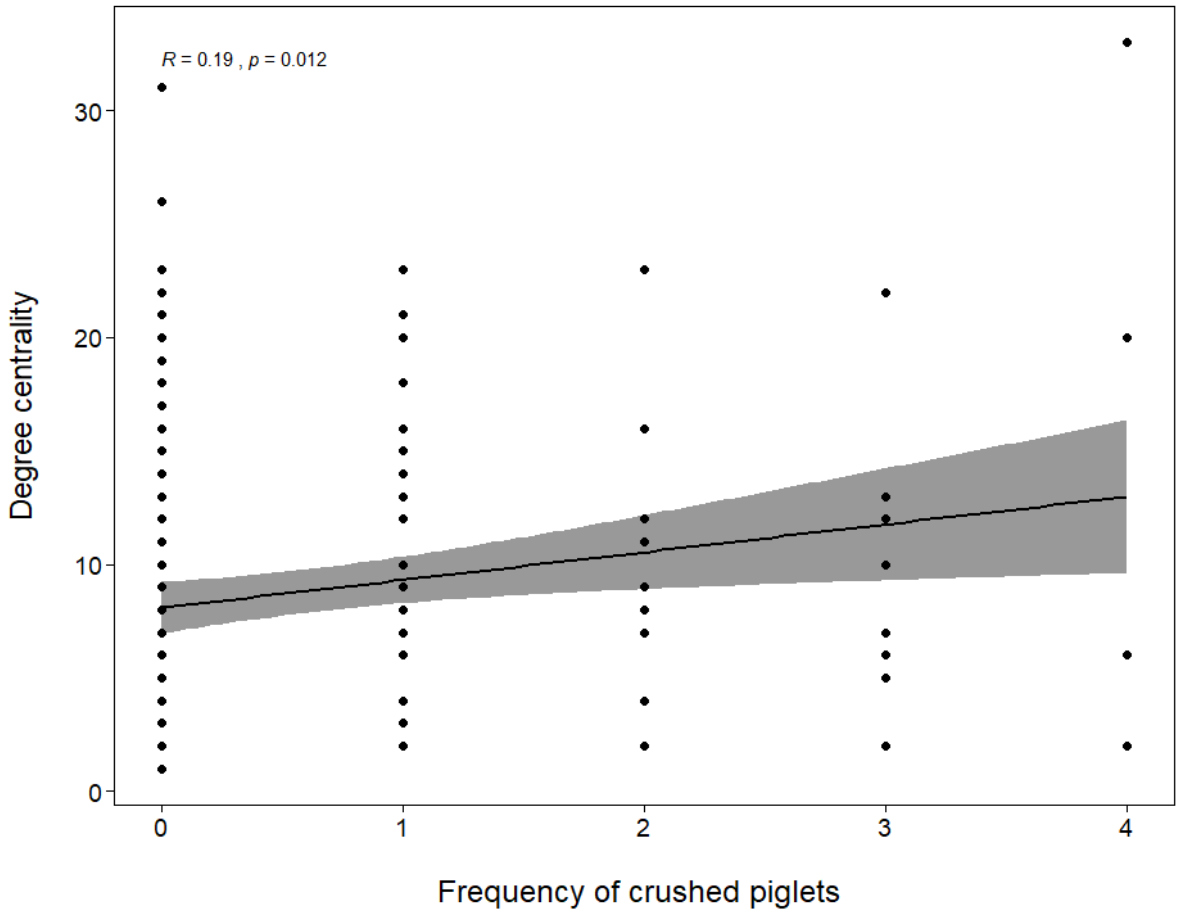

Figure 12. A weak, positive association occurred between the degree centrality and the frequency of crushed piglets using the data from all sows in the three production cycles (n=178). The association was significant. Degree centrality refers to the total number of initiated and received preferential associations.

5.3.3.4. Social prominence and the stability of production metrics over two farrowing events

Table 13. The mean frequency ± SD for stillbirths, mummified piglets, low viability piglets and crushed piglets for SPS quantified at least twice (n= 20), SPS quantified only once (n=34) and non-SPS (n=37) over the three production cycles. Data were taken from two farrowing events for each sow. The first farrowing event directly occurred after sows were removed from any of the three production cycles. The second farrowing event followed the first. SPS twice = sows were quantified prominent at least twice. SPS once = sows only quantified prominent once. Non-SPS = sows were never quantified prominent. SD = standard deviation.

Production metric	**Farrowing Event 1 Mean frequency ± SD**		**Farrowing Event 2 Mean frequency ± SD**	
Stillborn	SPS Twice:	0.6 ± 1.1	SPS Twice:	0.5 ± 0.7
	SPS Once:	2.0 ± 3.5	SPS Once:	1.4 ± 1.8
	Non-SPS:	1.9 ± 2.7	Non-SPS:	1.8 ± 1.9
Mummified	SPS Twice:	0.4 ± 0.8	SPS Twice:	0.4 ± 0.8
	SPS Once:	0.2 ± 0.5	SPS Once:	0.1 ± 0.3
	Non-SPS:	0.2 ± 0.7	Non-SPS:	0.1 ± 0.4
Low viability	SPS Twice:	0.6 ± 0.8	SPS Twice:	1.0 ± 1.6
	SPS Once:	**1.0 ± 1.3***	**SPS Once:**	**0.3 ± 0.8***
	Non-SPS:	0.7 ± 1.3	Non-SPS:	0.8 ± 1.6
Crushed	SPS Twice:	0.6 ± 0.8	SPS Twice:	0.5 ± 0.5
	SPS Once:	**0.6 ± 1.0***	**SPS Once:**	**1.4 ± 2.0***
	Non-SPS:	0.4 ± 1.0	Non-SPS:	0.6 ± 0.8

***p<0.05**

There were significant changes in the low viability piglet numbers over two farrowing events (coef. -1.06, z -2.839, p = 0.007) for SPS quantified once and crushing rates over two farrowing events (coef. 0.78, z 2.724, p = 0.009) for SPS quantified only once during the study. All other metrics remained stable for all classified sows

5.3.4. The identification of socially influential sows

Please refer to Table 10 in Chapter four that provides a detailed description of socially influential sows identified within the subgroups of PC1, PC2 and PC3. PC1 quantified 13 SIS, PC2 quantified 11 SIS and PC3 quantified 6 SIS. Table 10 shows the number of individuals, not specific individuals. Betweenness centrality data is weighted to account for times when sows were absent from a network.

5.3.5. Production metrics and social influence

Table 14. The mean frequency ± SD for live-born, prenatal and postpartum piglet mortality rates for SIS and Non-SIS in PC1 (n=70), PC2 (n=52) and PC3 (n=56). No significant differences were found between SIS and Non-SIS for any production metric over all three networks. SIS = Socially influential sow. Non-SIS = not quantified as socially influential. SD = Standard deviation from the mean. PC = production cycle.

Production metric	PC1 (n=70) Mean frequency ± SD	PC2 (n=52) Mean frequency ± SD	PC3 (n=56) Mean frequency ± SD
Live-born	SIS: 11.1 ± 3.9 Non-SIS: 12.4 ± 3.9	SIS: 12.6 ± 2.9 Non-SIS: 12.7 ± 3.5	SIS: 14.8 ± 1.5 Non-SIS: 12.7 ± 3.4
Stillborn	SIS: 0.5 ± 1.2 Non-SIS: 1.9 ± 3.1	SIS: 1.1 ± 1.4 Non-SIS: 1.8 ± 2.8	SIS: 2.2 ± 2.1 Non-SIS: 2.1 ± 3.3
Mummified foetuses	SIS: 0.2 ± 0.6 Non-SIS: 0.2 ± 0.6	SIS: 0.2 ± 0.6 Non-SIS: 0.2 ± 0.4	SIS: 0.3 ± 0.8 Non-SIS: 0.1 ± 0.4
Total prenatal mortality	SIS: 0.7 ± 1.2 Non-SIS: 2.1 ± 3.3	SIS: 1.3 ± 1.7 Non-SIS: 2.0 ± 2.8	SIS: 2.5 ± 2.4 Non-SIS: 2.1 ± 3.3
Low viability	SIS: 0.7 ± 1.4 Non-SIS: 0.8 ± 1.3	SIS: 1.1 ± 1.5 Non-SIS: 0.9 ± 1.4	SIS: 0.3 ± 0.8 Non-SIS: 1.0 ± 1.5
Crushed	SIS: 1.0 ± 1.3 Non-SIS: 0.6 ± 0.9	SIS: 0.3 ± 0.5 Non-SIS: 0.8 ± 1.2	SIS: 0.8 ± 0.8 Non-SIS: 0.5 ± 1.1
Total postpartum mortality	SIS: 2.5 ± 3.4 Non-SIS: 2.1 ± 2.1	SIS: 1.8 ± 1.9 Non-SIS: 2.2 ± 2.5	SIS: 1.2 ± 1.2 Non-SIS: 1.9 ± 2.2
Total piglet mortality	SIS: 3.6 ± 3.1 Non-SIS: 4.1 ± 3.5	SIS: 3.1 ± 2.9 Non-SIS: 4.2 ± 3.5	SIS: 3.7 ± 2.3 Non-SIS: 3.9 ± 3.8

5.3.6. The relationship between betweenness centrality and production metrics

The network centrality metrics of all three production cycles were combined to investigate an overall association between betweenness centrality and reproductive performance. Associations do not account for whether an individual is quantified SIS, instead refers only to the betweenness centrality data. Associations include every individual in all three production cycles, where

production data was available (n=178). An association was found between betweenness centrality and stillborn piglets (figure 13).

5.3.6.1. Betweenness centrality and live-born piglets

No association was found between betweenness centrality and numbers of live-born piglets, r_s = -0.071, p = 0.34. Live-born numbers remained stable and consistent over all three networks for both SIS and non-SIS with no significant effect of social role on live-born numbers (Table 14). Furthermore, there were no significant differences in litter size between SIS and non-SIS.

5.3.6.2. Betweenness centrality and prenatal mortality

There was no association between the overall betweenness centrality and prenatal mortality in all three networks. In PC1, there was a moderate negative association between the frequency of stillbirths and betweenness centrality, which was statistically significant, r_s= -0.37, p = 0.0016 (Figure 13). At an individual level, social role quantified by betweenness centrality did not impact upon stillbirth mortality rates (Table 14). No differences in betweenness centrality were found when all sows in every production cycle were categorised into being sows with stillborn piglets or sows without (coef. -0.36, z -1.424, p = 0.15).

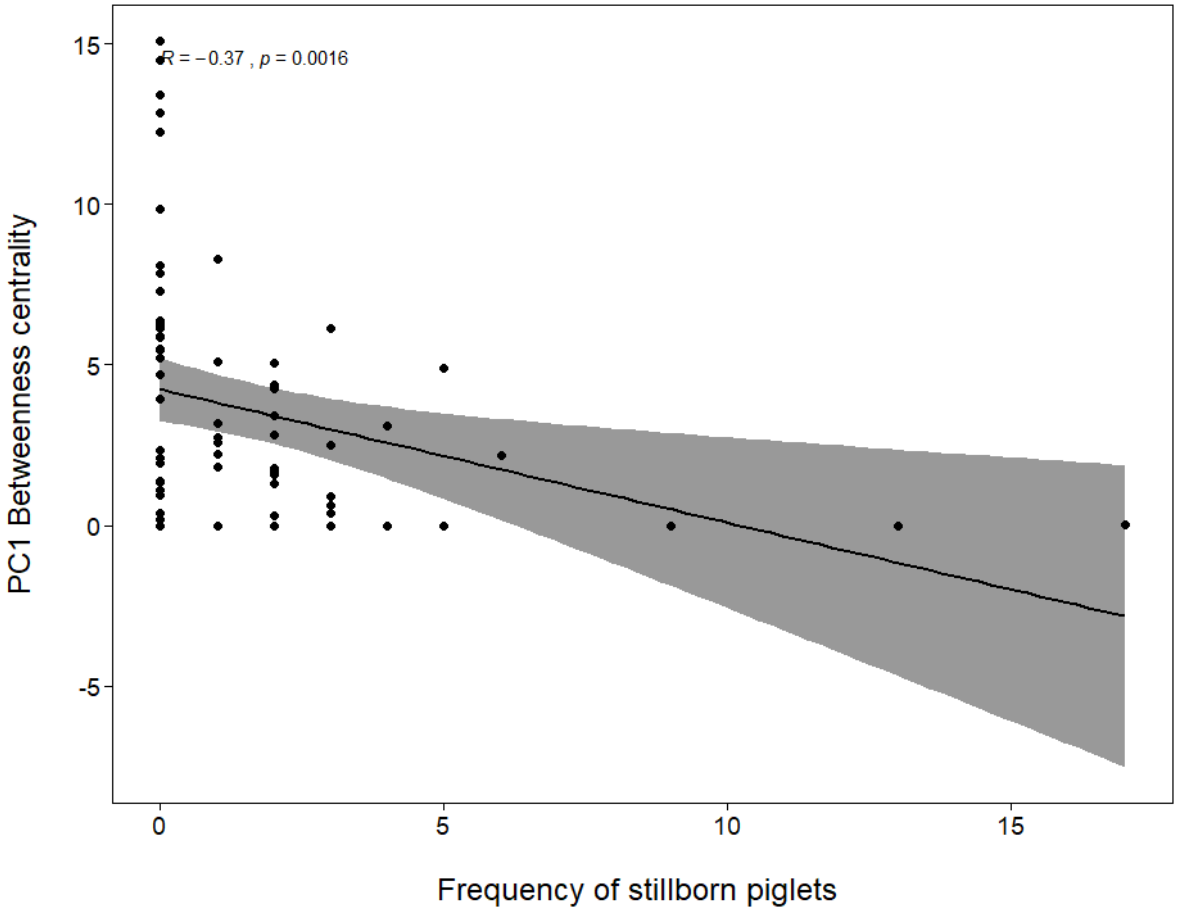

Figure 13. A moderate, positive association between the betweenness centrality of sows in PC1 (n=70) and the frequency of stillborn piglets. The association was significant. PC1 = Production cycle 1.

5.3.6.3. Betweenness centrality and postpartum mortality

There was no association between betweenness centrality and postpartum deaths rates in all three networks. In PC1, there was a weak positive association between the numbers of crushed piglets and betweenness centrality, that proved statistically significant, $r_s = 0.24$, $p = 0.04$ (Figure 14).

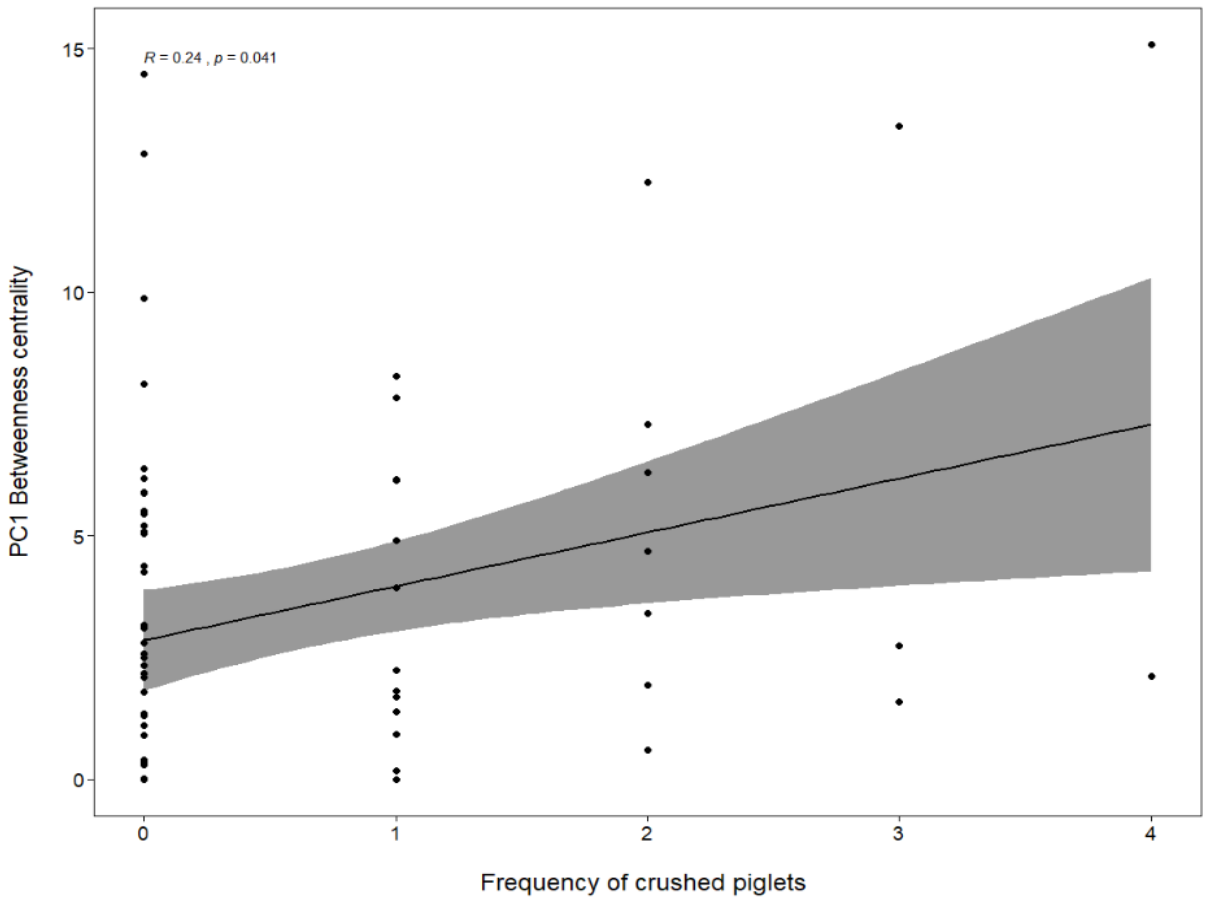

Figure 14. A weak, positive association between the betweenness centrality of sows in PC1 (n=70) and the frequency of crushed piglets. The association was significant. PC1 = Production cycle 1.

At an individual level, social role quantified by betweenness centrality did not impact crushing behaviour (Table 14). No differences in betweenness centrality were found when all sows in every production cycle were categorised into being crushing sows or non-crushing sows (coef. 0.35, z 1.474, p = 0.14).

5.3.6.4. Social influence and the stability of production metrics over two farrowing events

Table 15. The mean frequency ± SD for stillbirths, mummified piglets, low viability piglets and crushed piglets for SIS quantified at least twice (n= 3), SIS quantified only once (n=22) and non-SIS (n=53) over the three production cycles. Data were taken from two farrowing events for each sow. The first farrowing event occurred directly after a sow had been removed from any of the three production cycles. The second farrowing event followed the first. There were significant changes in stillbirths over two farrowing events (coef. 1.7o8e+01, z 7.589, p<0.001) for non-SIS. All other metrics remained stable for all classified sows. SIS twice = sows were quantified influential at least twice. SIS once = sows were only quantified influential once. Non-SIS = sows were never quantified influential. SD = standard deviation.

Production metric	**Farrowing Event 1 Mean frequency ± SD**		**Farrowing Event 2 Mean frequency ± SD**	
Stillborn	SIS Twice:	1.3 ± 1.5	SIS Twice:	N/A
	SIS Once:	1.3 ± 1.6	SIS Once:	1.3 ± 2.1
	Non-SIS:	**2.1 ± 3.2***	**Non-SIS:**	**1.4 ± 1.6***
Mummified	SIS Twice:	0.7 ± 1.2	SIS Twice:	N/A
	SIS Once:	0.1 ± 0.4	SIS Once:	0.2 ± 0.6
	Non-SIS:	0.2 ± 0.6	Non-SIS:	0.2 ± 0.5
Low viability	SIS Twice:	N/A	SIS Twice:	0.3 ± 0.6
	SIS Once:	0.7 ± 1.1	SIS Once:	0.8 ± 1.3
	Non-SIS:	0.8 ± 1.5	Non-SIS:	0.8 ± 1.3
Crushed	SIS Twice:	0.7 ± 0.6	SIS Twice:	0.3 ± 0.6
	SIS Once:	0.7 ± 1.1	SIS Once:	1.1 ± 1.6
	Non-SIS:	0.5 ± 1.0	Non-SIS:	0.8 ± 1.3

***p<0.05**

5.3.7. Effect of parity on production metrics

There was no effect of parity found on any of the postpartum production metrics or crushing behaviour. While there were also no differences in the numbers of mummified piglets over the parities, there were significant differences in stillbirths between older sows (parities five and six) and younger sows (parities two and three), coef. 1.37, z 2.825, $p < 0.05$. Older sows produced significantly higher rates of stillborn piglets than their younger conspecifics.

5.4. Discussion

The association between prosocial behaviours and reproductive fitness has been documented in a few wild species but so far has not been established in commercial animals. This study investigated the relationship between socio-positive centrality measures and numerous production metrics. Although the findings indicate an impact of social role on certain reproduction metrics, the results must be considered with caution. Weak correlations between the centrality metrics, stillbirths and crushing behaviour were, to an extent, anchored by a small number of individuals, whose removal may impart effects on the overall relationships. Despite this, an association between degree centrality and stillbirths were discovered with SPS consistently demonstrating lower rates of stillbirths than non-SPS over the three production cycles. This pattern of results is also seen between SIS and non-SIS in PC1 and PC2. Additionally, the study begins to show that consistency in network position is seemingly impacting on the levels of stillbirths. During the analysis of socio-positive centrality metrics, a noticeably weak negative relationship existed between degree centrality and stillborn piglets over the three production cycles. An additional association was found in PC1 between betweenness centrality and stillbirths. In all three production cycles, individuals quantified as SPS demonstrated lower rates of stillbirths compared to non-SPS, these differences tended towards statistical significance in PC1 and PC2. Additionally, in two of the networks, SIS was shown to have lower rates of stillbirths than non-SIS. Although no association was found between foetal mummification and network position, SPS in all three production cycles demonstrated a lower mean of overall prenatal piglet mortality than non-SPS. A similar pattern of results for SIS was shown in PC1 and PC2.

The weak correlation found between stillbirths and the centrality metrics might be explained by the need to assess production stability over multiple farrowing events. When a snapshot was taken of the relationship between degree centrality, betweenness centrality and the production metrics from only one farrowing event, associations were found to be weak. By comparison, when the cumulative effects of social position were analysed, the results revealed there were differences in stillbirths. Sows that had been SPS at least twice over the production cycles demonstrated markedly lower numbers of stillbirths over two farrowing events than those who had been SPS only once or non-SPS. Also, sows never quantified as SIS revealed a significant decrease in stillbirths between the first and second farrowing. The metrics for stillbirths remained stable over two farrowing events for SPS quantified twice, SPS quantified once and non-SPS in all three production cycles. Indicating some level of production predictability and the frequency of engaging in a specific network position. It may be that when evaluating associations, a snapshot of centrality and production metrics is insufficient. Suggesting a more longitudinal study of multiple farrowings is required to investigate further the impact on the frequency of exhibiting significantly higher centrality over time on reproductive performance.

Despite the limitations of the current study to present a longitudinal investigation over multiple farrowing events, the findings do tentatively suggest a relationship between network position and stillbirths. It could be argued that the stillbirth numbers observed were affected by intra-partum asphyxia (van Dijk et al., 2008), a leading cause of stillbirths, rather than engaging in preferential associations. Intra-partum asphyxia occurs due to high prolificacy (Raguvaran et al., 2017) and subsequent prolonged parturition (Udomchanya et al., 2019). Large litter sizes are the principal

factor determining increased rates of both foetal mummification and stillbirths (Borges et al., 2005; Canario et al., 2006). However, there were no significant differences in litter size between SPS and non-SPS or SIS and non-SIS. Although the results could not identify the exact determinant of stillbirth occurrence, no differences in litter size indicate that prominence and influence were not impactful upon stillbirth deaths resulting from prolonged parturition, a result of high uterine capacity. Therefore, the secondary predominant type of stillbirth causation must be considered, which occurs not intra-partum but towards the end of gestation, and is typically associated with reproductive pathogens (Christianson, 1992). Despite, the multitude of pathogens that can potentially affect levels of stillbirths, porcine parvovirus type 1 (PPV1) presents as the most endemic viral disruptor of reproductive processes in commercial herds (Boisvert et al., 2010; Ren et al., 2013). Research of wild boar and commercial pigs has found that some degree of transient passive immunity for PPV1 can occur in offspring (Paul et al., 1982; Fenati et al., 2009). Equally, the capacity for the development of intrauterine antibody formation in piglets is directly correlated to the serological status of the sow (Vigre et al., 2003), a process impacted upon by the neuroendocrine system. The correlation is a meaningful connection, as reproductive functions are fundamentally controlled by the neuroendocrine system (von Borell, 1995), with social stressors shown to disrupt the hormonal levels responsible for normal reproduction (Madej et al., 2005).

Exhibiting significantly higher degree centrality and betweenness centrality is generally unstable (see chapter four). Consequently, being either SPS or SIS is a transient trait because the differences between the production cycles indicate the impact of individual differences in the composition of the networks, thus changing the threshold required to be quantified as either SPS

or SIS. Despite the transient nature of being socially prominent or influential, specific individuals quantified as SPS or SIS more than once, and these individuals consistently exhibited lower rates of stillbirths. There may be cumulative effects between engaging in preferential associations during gestation and the adrenal effects on antibody formation. For example, the fetal piglets of sows engaging in higher levels of preferential associations over a sustained period could present with a reduced chance of intrauterine infection. The hypothesis shows the direct result of maintaining the balance of the neuroendocrine system required for reproductive success by attenuating social stressors through socio-positive interactions.

Therefore, while social stressors may disrupt normal prenatal development, engagement in positive behaviours, such as preferential associations may mitigate to some extent the social challenges faced by dynamic breeding sows, indirectly improving reproductive performance. To further support the mitigating effect of enhanced wellbeing on health, recent research has established a relationship between psychological wellbeing and antibody production. Reducing social stressors in pigs has been shown to improve antibody responses by investigating the effects of housing environment on immune protection and subsequent health and welfare. Piglets housed in barren conditions present with lower natural immunity to *Actinobacillus pleuropneumoniae* and porcine reproductive and respiratory syndrome virus than piglets exposed to enriched conditions (Luo et al., 2017). A result supported by the findings of other research (i.e., Merlot et al., 2012; Proudfoot and Habing, 2015; van Dixhoorn et al., 2016). Such a strong relationship between the psychological and biological sheds new light on the findings of this present research. Even though every gestating sow experienced an enriched environment, with *ad-libitum* access to substrate

and freedom of movement, the results show lower stillbirth numbers in sows with significantly higher degree centrality and to some extent betweenness centrality. More multidisciplinary research is warranted to investigate this relationship. Still, the potential insight would be invaluable for reducing piglet losses, which currently impart such a devastating effect on welfare and profit.

The farrowing environment is another factor that requires evaluation in response to the revealed differences in stillbirth numbers between quantified and non-quantified sows. The original stillbirth hypothesis (Baxter and Petherick, 1980) states that the endocrine changes associated with stressors due to confinement in crates would increase farrowing time, resulting in higher levels of stillbirths. By engaging in the numerous mechanisms of social support, i.e., preferential associations, a resistance to the social and environmental challenges faced by commercial species can be promoted (Reimert et al., 2014). For example, research of social deprivation in piglets found that the provision of social buffering during isolation, through access to a conspecific, decreased the plasma cortisol levels that occur with activation of the HPA axis (Kanitz et al., 2014; Tuchscherer et al., 2014). It could be expected that sows quantified as either SPS or SIS would present with increased resistance to the stressors associated with confinement directly before and during parturition, reducing farrowing time and subsequent stillbirth numbers, although the breaking of attachment bonds when transferred from the herd to a farrowing crate might also induce higher stress levels. Conversely, extensive research has demonstrated that confinement does not impact upon farrowing time, reproductive hormones, or rates of stillbirths in comparison

to loose housing (Cronin et al., 1994; Lawrence et al., 1995; Fraser et al., 1997; Kilbride et al., 2012).

Instead, the significant and prevailing trends found to increase parturition time and stillbirths, in addition to those already discussed are multiple. These causes include breed (van Dijk et al., 2005), the administration of oxytocin (Alonso-Spilsbury et al., 2004; Mota-Rojas et al., 2005), broken umbilical cord (Udomchanya et al., 2019), high parity (Vanderhaeghe et al., 2010a; Pandolfi et al., 2017), sow body condition (Maes et al., 2004), environmental temperature (Odehnalová et al., 2008) and piglet birth weight (Udomchanya et al., 2019). Although piglet birth weight is shown to be affected by social stressors during gestation (Kranendonk et al., 2006b), the current study did not record these measures. Therefore, this factor cannot be adequately assessed concerning the centrality metrics and subsequent network positions. Moreover, while significant differences presented in stillbirths between high and lower parity sows, results in chapter four documented that centrality metrics are not impacted upon by parity. Parity cannot account for the overall differences between stillbirths, SPS, non-SPS or SIS and, non-SIS.

No association was found between the centrality metrics and any of the preweaning causes of piglet mortality including, low viability, starvation, hypothermia, lameness, scours, or any other unknown factor. Furthermore, there were no significant differences in overall postpartum piglet mortality between SPS and non-SPS or between SIS, and non-SIS. The results suggest that engagement in preferential associations during gestation does not have a direct effect on neonatal piglet survival due to the outlined causes. Although the risk factors of piglet mortality via other

factors, beyond crushing, are higher in confined sows (Kilbride et al., 2012), the sample size of the current study must be taken into consideration as related studies of piglet mortality have been conducted using either an extensive sample size, multiple farms or multiple farrowings (Kilbride et al., 2012; King et al., 2019). Another consideration is death records, in which rarer deaths are often attributed to misclassification (Kilbride et al., 2012), particularly if not informed by a necropsy procedure. For example, the risk of crushing in starved, low viability or hypothermic piglets is increased, as such death may be directed attributed to crushing leaving the indirect cause of mortality undisclosed (Edwards and Baxter, 2015). As such, this study provides only a snapshot of these less common mortality causes taken from one farrowing.

The lack of differences in piglet mortality resulting from low viability, starvation and hypothermia are likely due to the similarities in litter size between sows quantified as either SPS and SIS and sows engaging in prosocial behaviours at a lower threshold. No significant differences were found in litter size in all three production cycles. Litter size at parturition is the predominant cause of low viability piglets. The intrapartum hypoxia experienced by neonates due to prolonged farrowing inhibits hippocampal neuron development (Singh et al., 2019) affecting future cognitive processes. As such, low viability piglets will face inordinate challenges in their capacity to access the levels of colostrum required for development and thermoregulation, which is related directly to starvation and hypothermia (Muns et al., 2016). Despite a lack of association between prominence and influence and preweaning mortality causes, the findings continue to suggest that the relationship between network position and stillbirths may be related to neuroendocrine activity, rather than litter size. Neonatal vitality is intrinsically correlated to intrapartum hypoxia and not infectious

causes (Trujillo-Ortega et al., 2007). Therefore, if the differences in stillbirths had been a direct result of litter size, there would be an expectation to have also seen significant differences in the numbers of low viability piglets of SPS and non-SPS or SIS, and non-SIS. The study presents an argument for the causal link between stillbirths and the effects of social interactions, although consideration must also be made of potential unknown variables that may have had an effect.

No association was discovered between the centrality metrics and lameness. Lameness in piglets typically relates to any clinical symptoms associated with the locomotor system attributed to a multitude of causes including genetics, nutrition, litter size and environment (Zoric et al., 2016). A significant proportion of lameness mortality is attributed to infections such as joint infections (Christensen, 1996), impacted upon by the extended time spent lying in the creep area and by the sow (Mouttotou and Green, 1999) and the resulting abrasions that can occur depending on the type of flooring (Zoric et al., 2009). Overall levels of lameness mortality reported in this study were low in all three production cycles and are potentially due to the flooring in the farrowing crate and creep area. At Sturgeons farm, farrowing crates adhere to standard dimensions, consisting of a fully slatted, plastic flooring with the provision of a heated creep area. By contrast, metal slats present the greatest threat to the development of limb injuries (Quinn et al., 2015). However, it must also be considered that no association between the centrality metrics and lameness was found due to the number of piglets included in the study and the findings limited to only one herd. Previous research into piglet lameness and overall mortality have included multiple farms and extensive numbers of piglets and sows (Christensen, 1996; Quinn et al., 2015; Sørensen et al., 2016). Finally, the presence of scours found on the study farm was rare, with no reports of

infection in PC2 and a low mean rate in PC1 and PC3; so, no association was found between the centrality metrics and scours. The causes of diarrhoea in suckling piglets are related to infections transmitted after parturition, with the primary protagonist being *Escherichia coli* (Nagy & Fekete, 1999). Individual resistance to disease is determined by consuming appropriate amounts of the protective antibodies found in colostrum (Devillers et al., 2011). Low viability piglets would be more susceptible to scours if they were unable to access the colostrum, however good hygiene and vaccination management would significantly reduce the presence of scour induced infections. Sturgeons farm operates stringent cleansing of farrowing crates following every weaning; the area is washed and disinfected with Virocid, a broad-spectrum disinfectant. Crate temperatures are computer regulated for the ideal sow comfort between 18 ^{o}C and 22 ^{o}C. Protection against *Escherichia coli* is provided with the provision of 2mg of Colicloss three weeks before weaning. Similarly, after weaning and before artificial insemination, every sow is vaccinated with Ery + Parvo (inactivated erysipelas and porcine parvovirus vaccine).

This study found a weak positive association between degree centrality and crushing behaviour (figure 12), despite no association found with betweenness centrality. The differences between the centrality metrics and crushing may be explained by the mechanism in which the metrics are measured. Degree centrality is the direct action of passing on or engaging in a behaviour, as such, sows with a high degree centrality will be more active within the context of the preferential association networks, demonstrating more changes from a standing to lying position. An individual with a tendency towards increased levels of standing-to-lying positions could present with an increased potential of piglet crushing (Vieuille et al., 2003). At a network position level, however,

only PC1 showed just significant differences between SPS and non-SPS. Previous research has documented a correlation between social behaviour and crushing events. Andersen et al. (2005) found that mothers who engaged in more exploratory behaviour (i.e., nosing) crushed significantly fewer piglets than sows who were less explorative. Outlined previously, socio-positive interactions increase resistance to social stressors during gestation enhancing reproductive fitness. By comparison, a reduced resistance can also impact upon maternal responses by increasing the frequency of sow posture changes postpartum (Rutherford et al., 2014), furthering the chance of overlays. Previous research would suggest that, within the current study, it could be expected that SPS and SIS would exhibit less crushing behaviour than non-SPS and non-SIS. However, the inconsistencies of the mean statistics over all three production cycles and the centrality metrics indicate a more precautionary approach to the findings is taken. The primary limitation and concern surround the farrowing environment, which inhibits the full expression of crushing behaviour due to physical restriction. By their very design, farrowing crates were introduced to reduce overlying (Fraser and Broom, 1990), as death by crushing is significantly higher in loose systems compared to restricted environments (Weber et al., 2007). Subsequently, in the current chapter, due to physical confinement during and after farrowing, another measure of establishing crushing propensity may have been more appropriate. A key measure to determine maternal behaviour that directly impacts upon crushing rates is the vocalisation responses of the sow to her litter. Communication is a highly significant predictor of active and positive maternal behaviour (Grimberg-Henrici et al., 2017) and is particularly fundamental in crushing events, as latency to respond to piglet distress calls will significantly impact upon survival. Piglet distress response tests

may be a more useful measure of crushing behaviour for future related research of sows housed in farrowing crates.

5.5. Conclusions

The predominant findings of this research have revealed that the frequency of stillborn piglets is consistently lower in SPS than non-SPS in all three preferential association networks and lower in SIS than non-SIS in PC1 and PC2. With no noteworthy differences presented in litter size between SPS and non-SPS or SIS and non-SIS, it points clearly towards another underlying causation for stillbirth mortality in the study herd. Despite limitations in the inability to directly correlate centrality metrics with multiple farrowing events, the results suggest that being socially prominent more than once decreased the numbers of stillbirths substantially. Supporting the suggestion that consistently engaging in significantly higher levels of socio-positive interactions is beneficial to reproductive processes, beyond the influence of environmental factors, that all sows were equally exposed to. Overall, being socially prominent was found to have a superior positive impact on stillbirths and adverse effects upon crushing behaviour than being socially influential. It also indicates that indirect socio-positive connections may have a less potent effect than direct interactions on these metrics. An important fact because the findings suggest that degree centrality is a more effective centrality metric then betweenness centrality to focus on in future related research.

Chapter Six:

Social prominence and influence in a dynamic breeding sow herd in three agonistic networks

6.1. Introduction

The abolishment of commercial farming sow stalls has seen an increase in the implementation of group-housing systems for breeding sows. While this transition has been a significant move forward for the improvement of welfare, it is aspect dependent. Group-housing allows for freedom of movement and the ability to perform natural behaviours; unfortunately, it also compromises welfare through aggression. This compromise is particularly relevant in dynamic systems such as the dry sow house in this study, where the frequent remixing of unfamiliar conspecifics into the herd destabilises the social group, increasing despotic behaviour as the social hierarchy is established (McGlone, 1985). To that end, extensive research has focussed on measures to reduce aggression and improve welfare, including an array of multidisciplinary approaches. These approaches include nutrition (Poletto et al., 2014), feeding methods (Bench et al., 2013a), space allowance (Remience et al., 2008), group size (Hodgkiss et al., 1998), stage of gestation at remixing (Stevens et al., 2015), boar presence (Barnett et al., 1993b), enrichment (Jensen et al., 2000) and pig appeasing pheromones (Plush et al., 2013).

The provision of management strategies to reduce short-term acute aggression after remixing is a significant element for improving wellbeing. The confined environment of group-housing allows for persistent chronic aggression in response to competition for critical resources. It is this chronic aggression that promotes long term detrimental effects on welfare and production (Marchant et al., 1995), beyond the physical injuries associated with the agonistic behaviours demonstrated directly after mixing (Peters, 1982). Despite the extensive knowledge acquired which serves to

guide interventions and management strategies, many methods are still failing to achieve the objective of reducing aggression, both in the short and long term (Marchant-Forde, 2010). As such, new directions must be undertaken to build upon the magnitude of research that is currently available. A recent study by Verdon et al. (2017) investigated group composition based upon aggressive predictive behaviour. The individual-centred approach highlighted the potential limitations associated with the application of the model-pig test, a result of context-specific complexities and is a finding supported by Turner et al., (2017); who concluded that initiating acute aggression after mixing was also not a predictor of long-term aggressiveness. Although evidence indicates there is the capacity for stable aggressive personalities in young pigs over short time frames (Erhard and Mendl, 1997), plasticity in social behaviour can also be a context-specific response, revealed in the instability of individual prosocial behaviour in chapter four and documented in the fluidity of aggression in a wide range of species (Jones et al., 2010; Ishikawa and Miura, 2012; Duncan et al., 2013; Nandy et al., 2016; Lehtonen and Wong, 2017; Baniel et al., 2018).

Group composition strategies provide an opportunity for targeted individual-centred methods to reduce aggression in commercial pigs. This is a technique employed in other captive species to maintain social stability and reproductive success by understanding the optimum social configuration (Dazey et al., 1977; Lemasson et al., 2005; Edwards et al., 2016; Jones et al., 2018). Effective strategies are dependent on the ability of aggressive tendencies to be investigated over time and social contexts to establish a more accurate perception of individual behaviour. When accounting for context-dependent aggression, it could be hypothesised that perceptions of the

aggressive tendencies of an individual at any given timeframe are variable, for example, personality tests, may not provide a true reflection of context-specific reactive behaviour. The capacity of social network analysis (SNA) to investigate temporal changes in behaviour at a group and individual level would provide a solution to the difficulties faced by previous studies (i.e., Verdon et al., 2018). SNA has previously been applied to research individual variation in the social personalities of lemurs (Kulahci et al., 2018a), the stability of affiliative and agonistic behaviours in dairy cattle (Foris et al., 2019) and personality, and power in rhesus macaque societies (McCowan et al., 2011). A growing body of SNA work also has developed in the study of pig aggression including changes in aggression following mixing (Büttner et al., 2015), context-specific responses (Agha et al., 2020) and predictions of future aggressive behaviours (Foister et al., 2018, Turner et al., 2020).

With the application of social network analysis, this study aims to identify socially prominent and socially influential individuals in the aggression networks of group-housed breeding dry sows. Inter and intra individual variations in behavioural strategies will be investigated by analysing the temporal changes in agonistic behaviours over three production cycles to ascertain the stability of aggressive traits at an individual and group level. The effect of parity on prominence and influence will be explored. Finally, due to the dynamic nature of the study herd, the impact of time spent in the herd and aggression will also be investigated.

6.2. Methods

Chapter two provides a detailed description of the methods. A summary is outlined in the following sections:

6.2.1. Animals and housing

The study was conducted at Sturgeons farm, Writtle University College, Chelmsford, Essex between November 2017, and January 2018. The study group consisted of a commercial cross of Large White-Landrace and Pietrain breeds; parities one to seven, in a dry sow barn. Sows were fed on a complete feed for breeding sows through electronic sow feeders, reset daily at 15:00 h, with additional access to *ad libitum* straw. Sturgeons farm operates a dynamic system in which small groups of sows are remixed into the herd every third Tuesday. There is a repeated cycle of production following the pattern, farrowing week, breeding week, and weaning week. For individual identification, each sow was marked with coloured dots and stripes, or both on their backs. Colour codes corresponded to ear-tag number.

6.2.2. Data collection

6.2.2.1. Sow data

The farm diaries and liaising with the pig unit manager provided relevant information concerning parity, farrowing date, date of remixing and remixing group.

6.2.2.2. Video observation data

A total of five CCTV H.265 4Mega Pixel Eyeball PoE, infrared Dome cameras were installed in the dry barn to capture and observe sow behaviour. Each camera was positioned to provide unobstructed, direct visual access to all essential functional areas (Chapter two, Figure 3). The areas included the straw bedded area, the passageway, the isolation pen, the ESF area and the nipple-drinkers. Three hours per day were selected for observation, 08:00-09:00 h, 15:00-16:00 h and 20:00-21:00 h. Observations occurred over three 21-day production cycles from 20th November 2017 to 21st January 2018. The video observations occurred on seven preselected days of each production cycle, including the day before remixing (day 20) and the day of mixing (day 21). The observations continued, on the three consecutive days following a mixing event (days 1,2,3). Days 7 and 14, following remixing, were also selected. Hereafter production cycle one, production cycle two and production cycle three will be referred to as PC1, PC2 and PC3, respectively. Overall, the study included 21 h of video footage for each production cycle providing 63 h of behaviours for analysis.

6.2.2.3. Social behaviours

The behaviour sampling method used an all-occurrences method of observation, considered the most effective and appropriate form of direct sampling method for observing rarer behaviours such as aggression (Martin and Bateman, 2007). The method is consistent with current, related research (i.e., Foris et al., 2018). Every occurrence of agonistic interactions (Table 16) was documented during the predetermined periods in PC1, PC2 and PC3. Behavioural observations recorded who attacked whom and if these interactions were reciprocated, allowing for the

construction of directed networks. The frequency of aggression was recorded to allow for a weighted representation of the three production cycles. No threshold measures were applied to the network, consistent with other social network analysis of aggression (i.e., Büttner et al., 2015) and all three production cycles reflect the original network compositions.

Table 16. Ethogram of agonistic behaviours. Adapted from Büttner et al., 2015; Camerlink et al., 2016a.

Behaviour	Description
Agonistic interactions	
Head to body thrust	With mouth closed, a rapid thrust with the head or snout against any part of the body of the receiver behind the ears.
Head-to-head thrust	With mouth closed, a rapid thrust with the head or snout against the head, neck, or ears of the receiver.
Biting	A bite from the aggressor to any part of the receiver's body when the aggressor's mouth is open.
Displacement	The immediate physical displacement of the receiver from its original location to another location following an agonistic interaction or displacement of the receiver from a sitting or lying position to a standing position.
Chasing	The physical displacement of the receiver from its original location to another zone within the dry barn followed by chasing behaviour of the initiator in which the aggressor moves beyond 1m from its original location.

6.2.3. Construction of the networks

6.2.3.1. Visualisation of the networks

Visualisations of the social networks for agonistic encounters in all three production cycles are shown as sociograms. The networks consist of directed ties, in which the initiator and recipient of the aggression are displayed, allowing for the visualisation of 'who attacked whom'. Although edges are not weighted in the sociograms, all networks recorded the frequency of indegree centrality (received ties) and outdegree centrality (initiated ties).

6.2.3.2. Identification of subgroups

K-cores have been applied to each aggression network in the production cycles to ascertain subgroups based upon connectedness. A *k*-core is a subgraph in which every node has degree *k* or more connections with other nodes within the subgraph (Borgatti et al., 2018).

6.2.3.3. Quantifying social prominence in the agonistic networks

Degree centrality can provide a measure of prominence within subgroups (Gero et al., 2013). Prominent animals with a significantly higher degree centrality than their conspecifics are consequently more highly connected (Verdolin et al., 2014). Within the agonistic networks in the three production cycles, sows with an outdegree centrality above the 95% range of outdegree centralities for their *k*-core subgroup quantified as socially prominent (adapted from Verdolin et al., 2014). Hereafter, quantified sows are referred to as socially prominent sows (SPS) and sows' not quantified SPS are referred to as non-SPS.

6.2.3.4. Quantifying social influence in the agonistic networks

Betweenness centrality can provide a measure of influence within and between subgroups (Lusseau and Newman, 2004). Individuals with a significantly higher betweenness centrality than their conspecifics are subsequently more influential. Within the agonistic networks in the three production cycles, sows with a betweenness centrality above the 95% confidence range of the betweenness centralities for their *k*-core subgroup quantified as socially influential (adapted from Verdolin et al., 2014). Hereafter, socially influential sows will be referred to as SIS and a sow not quantified as socially influential will be referred to as non-SIS.

6.2.3.5. The coefficient for quantifying SPS and SIS in the agonistic networks

Socially prominent and influential sows either identified as those individuals whose outdegree centrality or betweenness centrality or both fell above the 95% confidence interval range for their assigned subgroup (*k*-core). This method is consistent with previous social network research (i.e., Verdolin et al., 2014). These individuals quantified applying the following coefficient, $x \pm z * s/ \sqrt{n}$. Where:

x = Mean outdegree centrality or the betweenness centrality for the *k*-core

z = 1.96, for the 95% confidence interval

s = Standard deviation of the outdegree centrality or the betweenness centrality for the *k*-core

$\sqrt{n}$ = Square root of the *k*-core population total

6.2.4. Data analysis

Matrices of the aggression networks for each production cycle were constructed in Excel and imported into Ucinet 6, version 6.634 (Borgatti et al., 2002). Sociograms were created in NetDraw (Borgatti et al., 2002). The general network and individual network metrics analysed in Ucinet included centralisation, degree centrality and betweenness centrality and *k*-cores. Statistical analysis was performed in R.3.4.1 (R Development Core Team, 2017). Data was subsequently tested for normality via histograms and the Shapiro Wilks test. The data were found to be nonnormally distributed. General linear mixed models (GLMMs) were performed in R.3.4.1 using the R package lme4, version 1.1-21 (Bates et al., 2015) to test for changes in centrality metrics between production cycles, time spent in the herd and the effect of parity on social prominence or influence. Upon testing, the negative binomial model was found to be the best fit for the probability distribution. For each model, the pig identification number represented the random effects, and the fixed effects included mixing group, parity, and production cycle.

6.3. Results

6.3.1. Visualisation of the aggression networks: Socially prominent and influential sows

Sociograms illustrate the agonistic interactions between sows over PC1, PC2 and PC3. The sociograms display aggressive behaviours across seven predetermined days in each production cycle, with a total of 63 hours of behavioural observations recorded. The edges between nodes are directed and weighted. No thresholds were applied, and each sociogram represents the original

composition of sows for each production cycle. The sociograms represent complete and one-mode networks.

The sociograms illustrate the distribution of socially prominent sows (SPS) and socially influential sows (SIS) within all three networks (Figures 15a, 15b, 15c). In PC1 (n=78), 27% (n=21) of the total population quantified as SPS and 29% (n=23) quantified as SIS. Only 10% (n=8) of the network identified as both SPS and SIS. In PC2 (n=78), 22% (n=17) of the herd quantified as SPS and 26% (n=20) quantified as SIS. Only 10% (n=8) of the network classified as both SPS and SIS. In PC3 (n=80), 20% (n=16) of the network quantified as SPS and 28% (n=22) quantified as SIS. Only 9% (n=7) of the herd identified as both SPS and SIS. Results are outlined in Table 17.

Table 17. An overview of the number of sows quantified as either socially prominent or influential in production cycle 1, production cycle 2 and production cycle 3 in the aggression networks.

	Production cycle 1 N = 78	Production cycle 2 N = 78	Production cycle 3 N = 80
Socially prominent sows (SPS)	21	17	16
Socially influential sows (SIS)	23	20	22
Both SPS and SIS	8	8	7

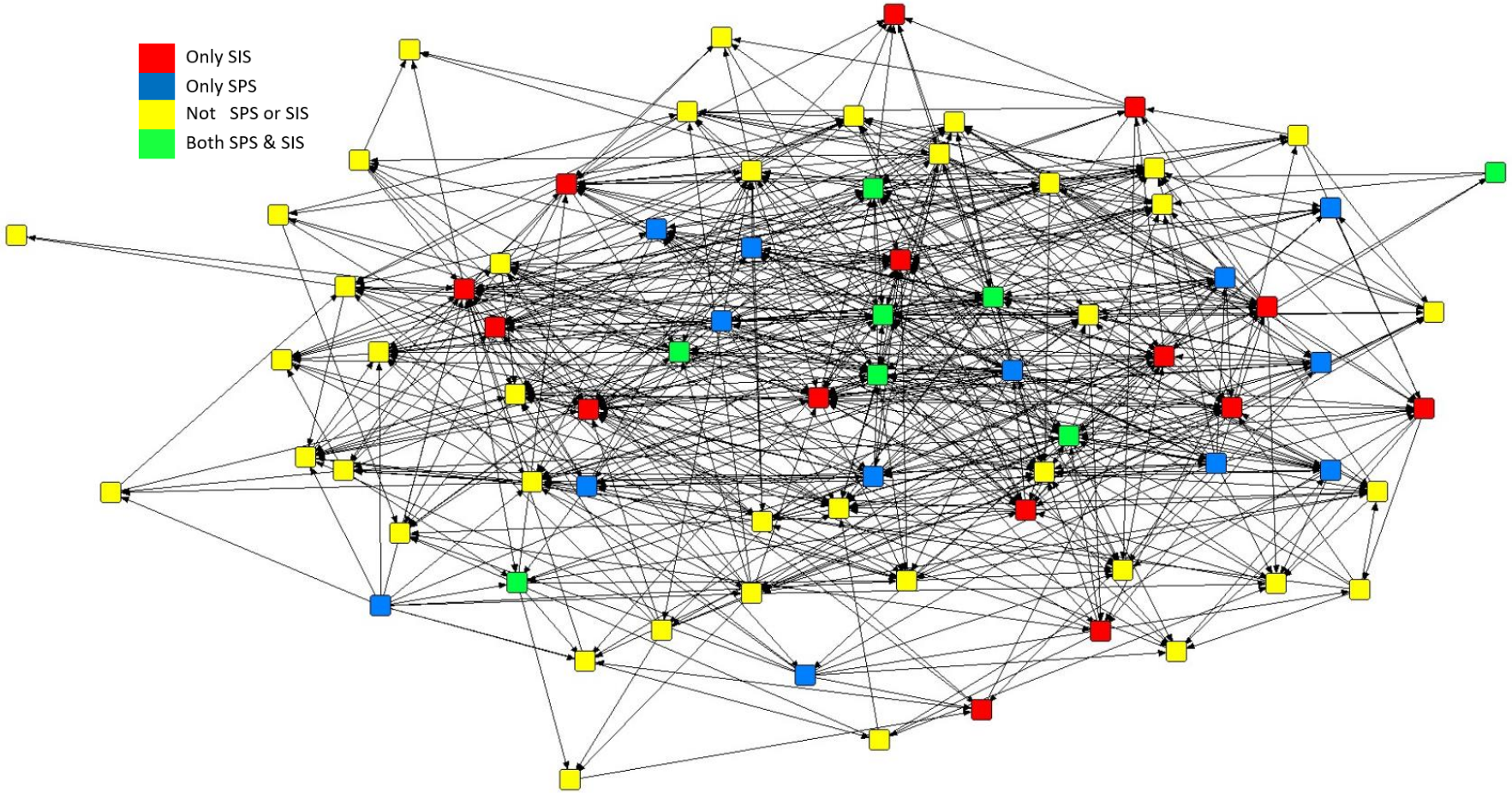

Figure 15a. Directed sociogram of agonistic interactions between dry-housed gestating sows for production cycle 1 (n=78). Behaviours occurred at Sturgeons farm, Writtle University College, Essex between 20th November and 10th December 2017. Sociogram displays sows quantified as only socially prominent (Only SPS, n=13), only socially influential (Only SIS, n=15), both socially prominent and influential (Both SPS & SIS, n=8) and not socially prominent or influential (Not SPS or SIS, n=42).

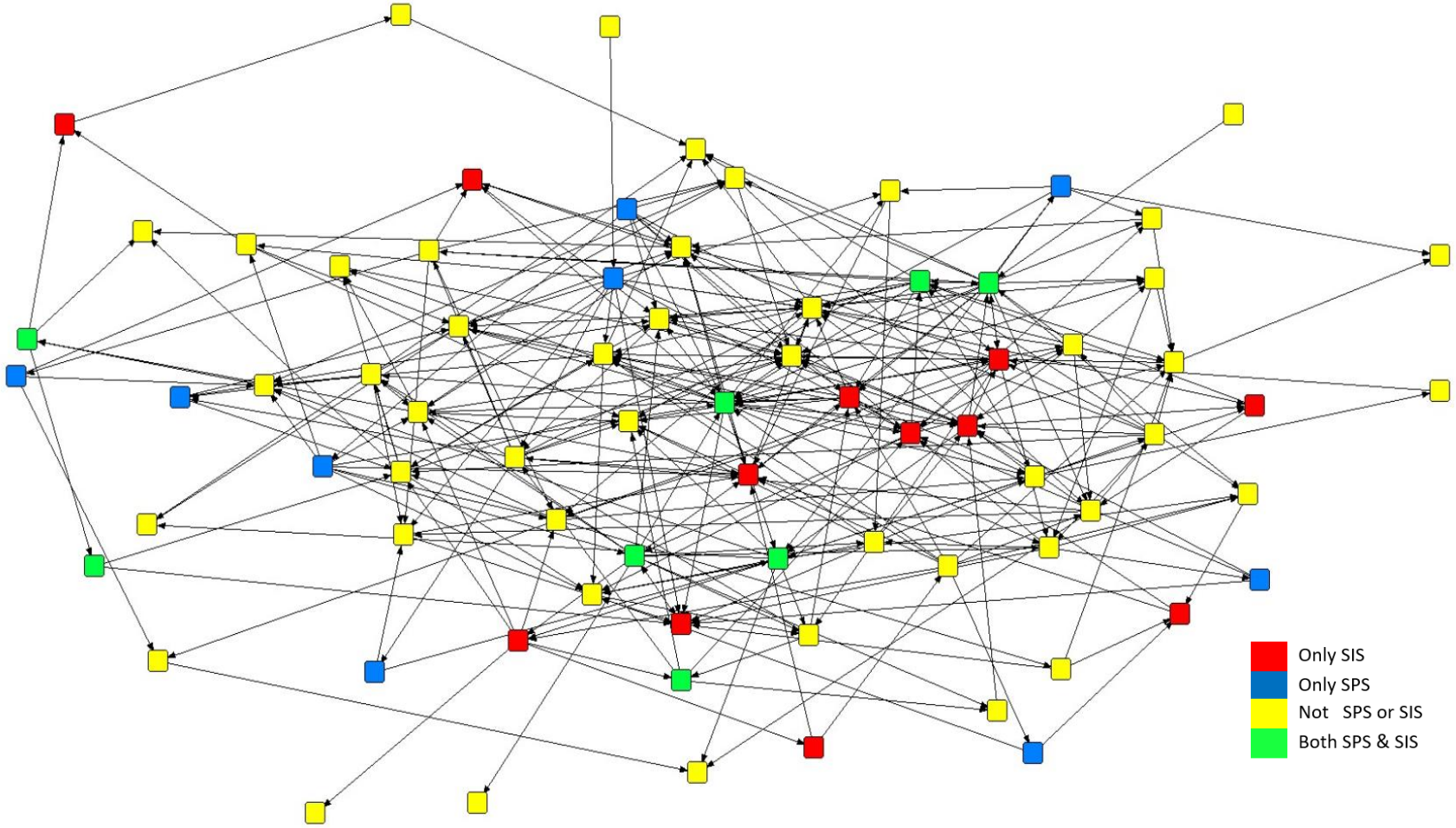

Figure 15b Directed sociogram of agonistic interactions between dry-housed gestating sows for production cycle 2 (n=78). Behaviours occurred at Sturgeons farm, Writtle University College, Essex between 11th December and 31st December 2017. Sociogram shows sows quantified as only socially prominent (Only SPS, n=9), only socially influential (Only SIS, n=12), both socially prominent and influential (Both SPS & SIS, n=8) and not socially prominent or influential (Not SPS or SIS, n=49).

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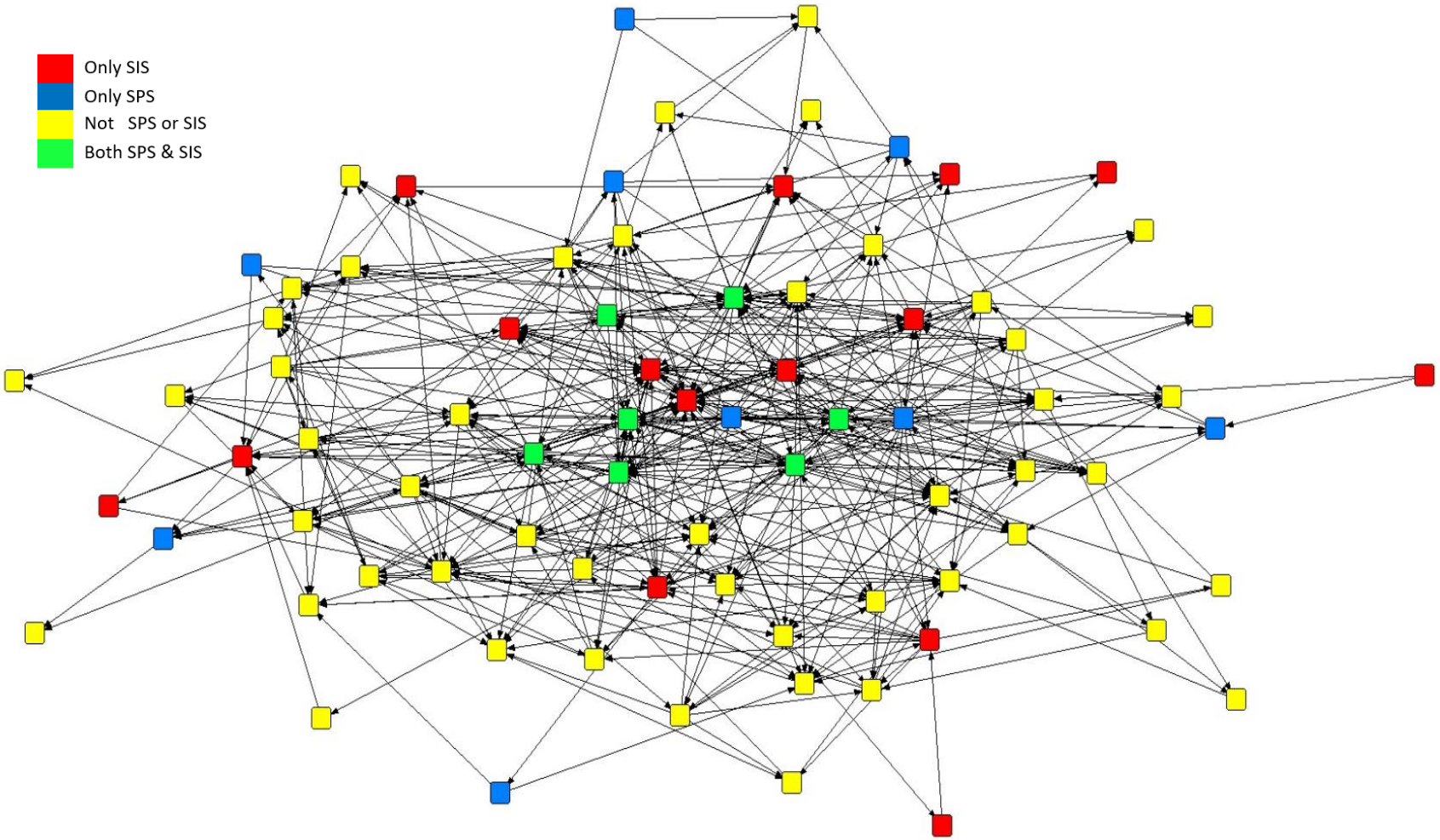


Figure 15c. Directed sociogram of agonistic interactions between dry-housed gestating sows for production cycle 3 (n=80). Behaviours occurred at Sturgeons farm, Writtle University College, Essex between 1st January and 21st January 2018. Sociogram shows sows quantified as only socially prominent (Only SPS, n=9), only socially influential (Only SIS, n=15), both socially prominent and influential (Both SPS & SIS, n=7) and not socially prominent or influential (Not SPS or SIS, n=49).

6.3.2. Quantifying missing data

Due to the dynamic nature of the herd, all sows were not consistently present during the 63 hours of observations, a result of remixing new sows or removing sows for farrowing. The data had to be weighted to account for the hours that individuals were missing from the study. In PC1, 15% of the herd (n=12) were missing from the network for 6 hours. In PC2, 15% of the population (n=12) were missing from the network for 6 hours, and 5% (n=4) were missing for 3 hours. In PC3, 15% of the herd (n=12) were absent from the network for 6 hours, with only one sow missing for 3 hours. The coefficient applied to both degree centrality, and betweenness centrality for absent sows is,

$y = n/x$.

Where: y = weighted value of interactions per hour observed

n = value of either degree centrality or betweenness centrality

x = number of hours observed

6.3.3. Social prominence in the subgroups

Table 18. The number of individuals, not specific individuals, within each *k*-core for PC1 (n=78), PC2 (n=78) and PC3 (n=80) quantified as SPS. These SPS had a degree centrality above the 95% confidence interval range for their subgroup. PC1 had a total of 21 SPS identified, which represented 27% of the network. The most connected subgroup (K10) contained the most SPS. PC2 had a total of 17 SPS identified, which represented 22% of the network. The most connected subgroup (K6) contained the most SPS. PC3 had a total of 16 SPS identified, which represented 20% of the network. The most connected subgroup also contained the most SPS. The *K* values, i.e., K10, refer to the subgroups, the coreness value represents how many individuals the sow is connected. For example, a K10 sow will be connected to at least ten other sows who are in turn connected to at least ten other sows in the aggression networks. PC1 shows a decentralised network compared to PC2 and PC3.

Production Cycle and *K*-core	**Outdegree Centrality mean ± SD**	**95% Confidence interval range**	**Number of socially prominent sows (SPS)**
Cycle 1			
Centralisation: 0.36			
K10	15.6 ± 10.4	12.7 – 18.5	16
K9	5.5 ± 2.4	3.6 – 7.4	1
K8	6.6 ± 3.0	4.7 – 8.5	3
K4	1.3 ± 1.5	0.0 -3.0	1
Total			**21**
Cycle 2			
Centralisation: 0.66			
K6	8.0 ± 7.8	5.6 – 10.4	8
K5	1.7 ± 1.6	1.7 – 3.7	3
K4	1.5 ± 3.7	1.5 – 3.7	1
K3	1.8 ± 1.3	0.7 – 2.9	5
Total			**17**
Cycle 3			
Centralisation: 0.81			
K8	12 ± 10.6	8.9 – 15.1	9
K7	4.0 ± 2.2	2.4 – 5.6	1
K6	3.7 ± 3.2	1.1 – 6.3	2
K5	1.4 ± 1.1	0.4 – 2.4	1
K4	2.0 ± 1.4	1.0 – 3.0	1
K3	1.3 ± 1.3	0.4 – 2.2	2
Total			**16**

The frequency of SPS remained consistent over all three production cycles despite considerable variation in the individual aggressiveness of SPS quantified in each (Figure 16). SPS in PC1 were shown to be more aggressive than in the other two networks and revealed two outliers. PC1 and PC2 SPS showed less within network variation in aggressive tendencies than in PC3. One outlier was identified in both PC2 and PC3, which demonstrated a markedly higher mean outdegree than the rest of the group.

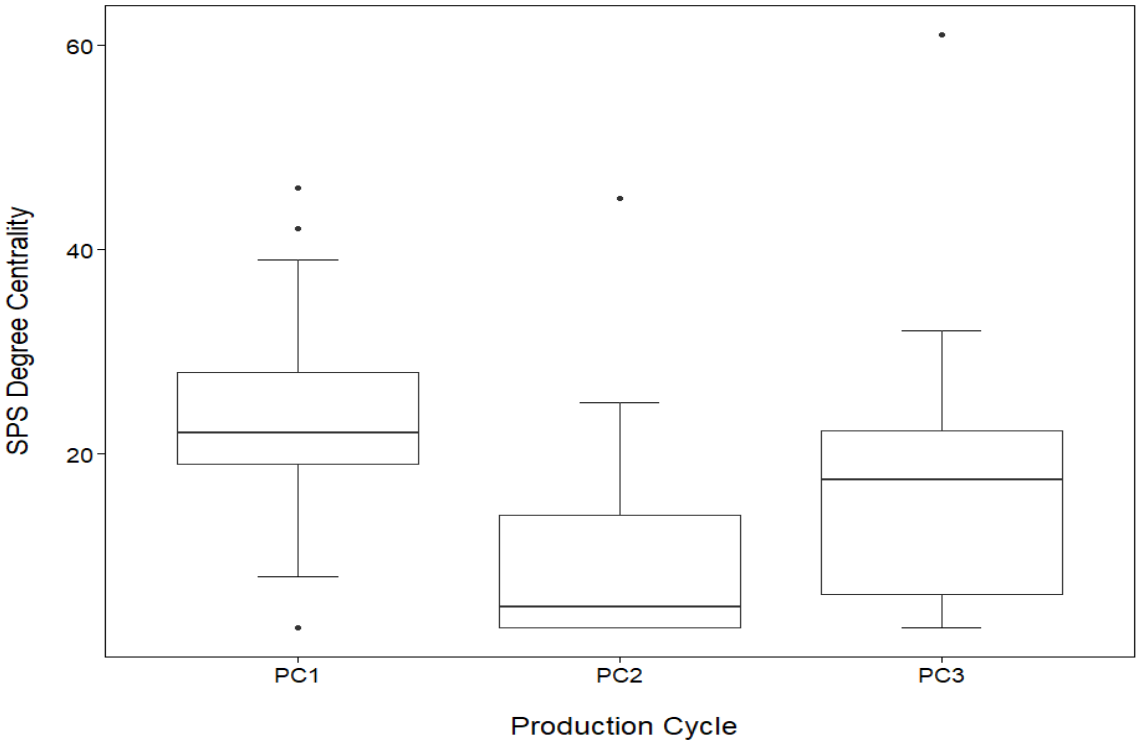


Figure 16. Outdegree centrality quartiles (based on initiated agonistic interactions) for all three production cycles. SPS quantified in PC1 (n= 21) had a median outdegree value of 22 and 48% (n=10) had an outdegree centrality above the median. The maximum outdegree centrality was 46 with a minimum value of 3, giving a range of 43.PC1 revealed two outliers above and one below. SPS quantified in PC2 (n=17) had a median outdegree value of 5 and 47% (n=8) had an outdegree centrality above the median. The maximum outdegree centrality was 45 with a minimum value of 3, giving a range of 42. PC2 revealed one outlier. SPS quantified in PC3 (n=16) had a median outdegree centrality of 17.5 and 44% (n=7) had an outdegree centrality above the median. The maximum outdegree centrality was 61 with a minimum value of 3, giving a range of 58. PC3 revealed one outlier.

6.3.4. Social influence in the subgroups

Table 19. The number of individuals, not specific individuals, within each *k*-core for PC1 (n=78), PC2 (n=78) and PC3 (n=80) quantified as SIS. These SPS had a degree centrality above the 95% confidence interval range for their subgroup. PC1 had a total of 23 SIS identified, which represented 29% of the network. The most connected subgroup (K10) contained the most SIS. PC2 had a total of 20 SIS identified, which represented 26% of the network. The most connected subgroup (K6) included the most SIS. PC3 had a total of 22 SIS identified, which represented 28% of the network. The most connected subgroup also contained the most SIS. The *k* values, i.e., K10, refer to the subgroups, the coreness value represents how many individuals the sow is connected. For example, a K10 sow will be connected to at least ten other sows who are in turn connected to at least ten other sows in the aggression networks.

Production Cycle and *K*-core	**Betweenness Centrality mean ± SD**	**95% Confidence interval range**	**Number of socially influential sows (SIS)**
Cycle 1			
K10	2.5 ± 1.7	2.0 -3.0	16
K9	1.3 ± 0.9	0.6 – 2.0	1
K8	0.9 ± 0.7	0.5 – 1.3	3
K7	0.3 ± 0.1	0.2 – 0.4	1
K6	0.6 ± 0.5	0.2 – 1.0	1
K4	0.1 ± 0.1	0.0 – 0.2	1
Total			**23**
Cycle 2			
K6	3.6 ± 2.5	2.5 – 4.7	12
K5	0.8 ± 0.6	0.4 – 1.2	3
K4	0.5 ± 0.8	0.0 – 1.2	1
K3	0.8 ± 1.2	0.1 – 1.5	3
K2	0.4 ± 0.7	0.0 – 1.1	1
Total			**20**
Cycle 3			
K8	3.1 ± 2.7	2.3 – 3.9	14
K7	2.4 ± 2.5	0.5 – 4.3	2
K6	1.2 ± 1.1	0.3 – 2.1	1
K5	0.6 ± 0.5	0.2 – 1.0	1
K4	0.9 ± 1.5	0.0 – 2.0	1
K3	0.04 ± 0.1	0.01 – 0.1	2
K2	0.1 ± 0.1	0.0 – 0.2	1
Total			**22**

The numbers of socially influential sows were consistent over all three production cycles, despite variation in the betweenness centrality showing between networks (Figure 17). Despite a proportion of the same sows observed in PC2 and PC3, sows in PC2 demonstrated a higher median value of betweenness centrality.

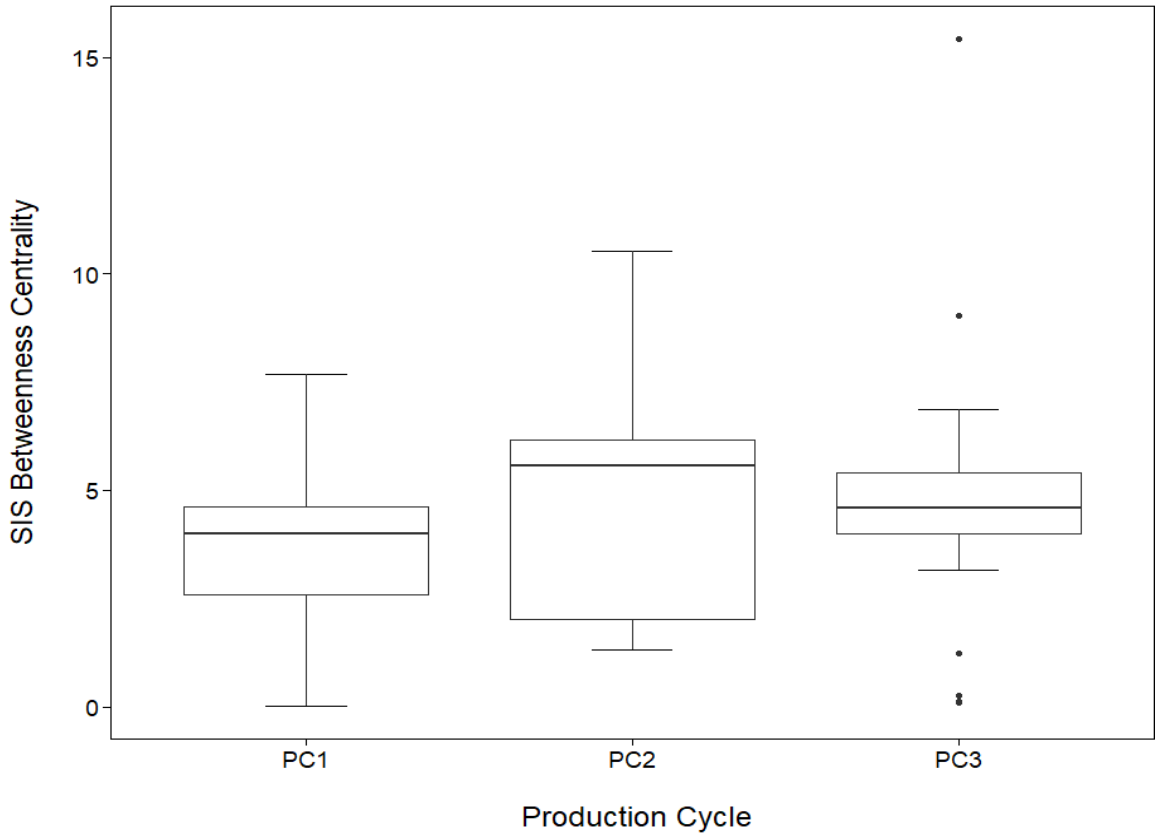


Figure 17. Betweenness centrality quartiles (based on initiated agonistic interactions) for all three production cycles. SIS quantified in PC1 (n= 23) had a median betweenness value of 4.01 and 48% (n=11) had a betweenness centrality above the median. The maximum betweenness centrality was 7.67, with a minimum value of 0.03, giving a range of 7.64. SIS quantified in PC2 (n=20) had a median betweenness value of 5.57 and 45% (n=9) had a betweenness centrality above the median. The maximum betweenness centrality was 10.53 with a minimum value of 1.3, giving a range of 9.23. SIS quantified in PC3 (n=22) had a median betweenness centrality of 4.61 and 45% (n=10) had a betweenness centrality above the median. The maximum betweenness centrality was 15.62 with a minimum value of 0.09, giving a range of 15.53. PC3 revealed five outliers.

6.3.5. Stability of social prominence and influence

6.3.5.1. Individual stability of being socially prominent

Inside the aggression networks, 32% (n=12) quantified as SPS 33% of the time, 26% (n=10) were SPS 50% of the time they were in the networks, 24% (n=9) quantified 67% of the time, and 18% (n=7) were SPS 100% of the time. Results indicate being socially prominent was generally temporary. Individuals showed a significant decrease in outdegree centrality between PC1 and PC2 (coef. -0.61, z -3.501, $p < 0.001$); with behaviour more stable between PC2 and PC3 (coef. 0.06, z 0.24, $p = 0.81$). Results do not represent a deviation from chance, X2 (2, n = 236) = 1.29, $p = 0.52$.

6.3.5.2. Individual stability of being socially influential

Overall, social influence was generally revealed to be unstable, 42% (n=20) quantified as SIS 33% of the time, 30% (n=14) 50% of the time, 11% (n=5) were SIS 67% of the time they were in the networks and 17% (n=8) quantified as SIS 100% of the time. In contrast, although SIS quantification was unstable, at an individual level, betweenness centrality was a stable social metric. Individuals did not significantly alter their behaviour between PC1 and PC2 (coef. -0.09, z -0.528, $p = 0.61$) or between PC2 and PC3 (coef. -0.21, z-1.243, $p = 0.21$). Results do not represent a deviation from chance, X2 (2, n = 236) = 1.35, $p = 0.51$.

6.3.6. The effect of parity on aggressiveness

All sows exhibited significantly more aggression compared to gilts, coef. 0.84, z 2.707, $p < 0.05$ and the eldest sows, with parity of seven, were significantly more aggressive than any of the parities in

the networks, coef. 1.31, z 2.629, $p< 0.05$. Results indicate that parity impacts upon outdegree centrality in an aggression network, with the levels of initiated aggression increasing with age. All sows exhibited significantly higher levels of betweenness centrality compared to gilts, coef. 1.04, z 3.360, $p < 0.01$. Although there were no significant differences between most of the parities above gilt level, parity six sows displayed higher betweenness centrality than parity three, four and five sows, coef. 0.42, z 2.461, $p < 0.05$.

6.3.7. Aggressiveness and time spent in the network

Newly remixed sows were less aggressive than resident sows, showing significantly lower levels of outdegree centrality, coef. -0.8, z -4.497, $p < 0.001$ and betweenness centrality, coef. -0.46, z -2.738, $p < 0.01$. New sows revealed a mean betweenness centrality of 1.42 ± 1.51SD compared to resident sows, 2.16 ± 2.32SD. New sows revealed a mean outdegree centrality of 4.17 ± 3.88SD compared to resident sows, 8.67 ± 9.57SD.

6.4. Discussion

The current study aimed to identify socially prominent and influential individuals in three aggression networks of breeding dry sows to ascertain the stability of behavioural strategies in response to a dynamic environment. The key findings showed SPS, and SIS were present in all three production cycles, and pigs did not have to be highly connected (i.e., coreness value) to be quantified as either prominent or influential. Outdegree centrality metrics, representing initiated aggression, were not stable over time at an individual or group level, while betweenness centrality

was established to be more stable for those identified as SIS. In contrast to the preferential association networks investigated in Chapter four (Table 9), the aggression networks demonstrated more centralisation (Table 18), particularly in PC2 and PC3. PC3 reflected the highest level of centralisation shown in the individual variance of initiated aggression between quantified SPS. Although all three networks showed that the majority of SPS and SIS existed within the most connected subgroup, PC1 outdegree centrality metrics revealed that SPS in K10 dominated the network (Table 18). This finding would explain the differences in centralisation between PC1 and the other two networks, as there were substantially more sows in the highest connected subgroup in PC1 and these individuals were also more aggressive than the sows in the highest connected subgroups in PC2 and PC3. Additionally, SPS in PC2 and PC3 were more evenly distributed throughout the herd.

As with the prosocial networks in Chapter four (Table 9 and Table 10), the socio-negative networks demonstrated stability in the numbers of individuals who quantified as either SPS or SIS over all three production cycles. This result is again showing a natural consistency in social structure despite individual changes in prominence or influence in each network. Chapter four (Table 9 and Table 10) and the current chapter (Table 18 and Table 19) revealed consistent numbers of SPS and SIS in all three production cycles, despite considerable differences between the centralisation values in the preferential association networks (PC1: 0.13, PC2: 0.05, PC3: 0.07) and the centralisation values in the aggression networks (PC1: 0.36, PC2: 0.66, PC3: 0.81). The consistencies of SPS and SIS in both behavioural networks in conjunction with considerable

variability in centralisation indicate that centralisation alone is not a useful predictor of the frequency of SPS or SIS that might be expected.

The general instability of the centrality metrics indicates a level of context dependent behaviour in response to an unpredictable dynamic social environment. Changes in aggression at an individual level impacted the overall observations of agonistic encounters between the production cycles, for example, socially prominent sows in production cycle 1 were shown to be more aggressive than those in production cycle 2 and production cycle 3. In comparison to the substantially lower rate of preferential interactions observed in chapter four, the findings also show that the Sturgeons farm sows are seemingly more motivated to establish and maintain the social dynamic through the application of high levels of aggression rather than positive behaviours. An unsurprising result, as acute aggression after mixing serves to stabilise the herd and reduce chronic aggression (Desire et al., 2015).

The findings continue to highlight that management strategies are the fundamental protagonist for the levels of aggression. Witnessed not just in commercial pigs but other domestic species, which also do not innately implement high levels of aggression to maintain social cohesion (i.e., horses, *Equus caballus*, Fureix et al., 2012; dairy cattle, *Bos taurus*, Costa et al., 2016). Extension to the understanding of reactive behaviour to challenging environments is critical for the development of group composition methods based upon individual differences. Therefore, the ability to form predictions of behaviour both at a group and individual level is essential. This study shows that at a group level, it can be predicted that there will be SPS and SIS in any aggression

network, distributed throughout the subgroups in the herd (based upon connectedness) and that the numbers of these individuals remain stable. The distribution of extremely aggressive sows throughout the herd is consistent with the proposal that as group size increases, beyond the point to which a clear social hierarchy can be achieved, the formation of subgroups will develop (Gonyou, 2001). The Sturgeons farm sows are forming subgroups, through whom they choose to connect with, a strategy which allows for conspecific avoidance when the costs of aggressive encounters may be too high. Variation in the thresholds of *k*-cores and numbers in each subgroup between production cycles is also consistent with the plasticity of behaviour documented in pigs in large social groups (Andersen et al., 2004; Samarakone and Gonyou, 2009).

Individual-level interpretation becomes more complex, as demonstrated in the instability of outdegree centrality. Results for the stability of being socially prominent were variable across the production cycles. SPS in PC1 did not continue to be as aggressive in the following production cycle, revealing a significant reduction in the levels of their initiated aggression in PC2 (section 6.3.5.1.). In contrast, SPS in PC2 demonstrated more stable behaviour continuing to be as aggressive in the following production cycle (section 6.3.5.1.). There were no significant differences in the outdegree centrality between PC2 and PC3. However, being socially prominent was not a stable trait, as only 28% of all SPS held the position more than once. As with the prosocial networks in Chapter four, social prominence is a transient trait because changing the configuration of the individuals in a network will alter the threshold required to be quantified as SPS. For example, an aggressive sow in PC1 may remain consistently aggressive in PC2 but might not be quantified as SPS twice because more aggressive individuals have been mixed into the

herd. Despite this, the behaviour changes reflected in those quantified as SPS was also found at the group level, where no associations were discovered between the overall aggressive interactions between the networks, indicating that pigs have a high between-variability based upon their engagement in agonistic interactions.

It may be that individuals are predisposed to a level of aggressiveness, determined by genotype or phenotype, as measured in the traditional tests for this behavioural trait. Still, predetermining individual aggressiveness as a foundation for group composition strategies based upon these conventional tests will not account for context-specific behaviour or different types of aggression. For example, Erhard et al., (1997) measured the individual aggressiveness of post-weaned pigs through the application of a resident-intruder test, proposing that grouping low-aggressive pigs together is the optimum configuration for reducing aggression after mixing. However, the study did not differentiate between defensive and offensive aggression. Reactions to a resident-intruder test reflect defensive aggression, which is shown to be independent of offensive aggression (Blumstein et al., 2012). The evidence is also indicating that individual-level decision making forms judgements when initiating behaviours in response to the assessment of the costs and benefits involved in specific social interactions. Research continues to indicate that there is behavioural fluidity when challenged with environmental or social changes which support the findings of this study. Estevez et al., (2002) found that domestic fowl, *Gallus gallus domesticus*, demonstrate plasticity in aggression relative to the costs and benefits of the behaviour in any given context, such as space allocation or feed availability. Applying the measure of degree centrality at any given time may provide a snapshot of which individuals are presently socially prominent in an

aggression network. It appears that when considering the dynamic systems faced by commercial animals, this metric is not a good predictor of future aggressive behaviour in dynamic breeding sows. A more powerful tool to extend upon the limitations of degree centrality in future related studies could be the application of eigenvector centrality, which like degree centrality, counts the number of node connections but additionally weights the nodes by their centrality. For example, Borgatti et al (2018) describes eigenvector centrality as '*a measure of popularity, a node with high eigenvector centrality is connected to nodes that are themselves well connected. This means that a node with a small degree could have a higher score than a node with a high degree if the first node's friends are very popular while the second node's friends are not*'.

In comparison, betweenness centrality was found to be a more stable metric, as there were no significant differences in the centrality metrics over time. SIS in PC1 revealed stable betweenness centrality in PC2, with a similar pattern of results for SIS in PC2 and the following production cycle (section 6.3.5.2.). The instability of the outdegree metrics shows that if a pig is aggressive in one network, it does not necessarily remain aggressive in the next. The evidence suggests though that if individuals act as a significant bridge in one network, they will continue to do so in the following. A key finding as it indicates that indirect interactions are more relevant to aggression networks than preferential association networks; chapter four found instability in the betweenness centrality of SIS over time. The result is due to the mechanism of indirect interactions as a process for enabling the flow of behaviour through a network in the study herd, aggression was the most prolific behaviour. Furthermore, identifying influential behaviour as being more stable than prominence is critical for evaluating

aggression networks because of the reach factor (Watling et al., 2015). For example, direct interactions are dyadic and therefore, once an interaction occurs, no other individuals can be involved or affected by the behavioural exchange. By comparison, betweenness centrality extends beyond the dyadic and can reach many more individuals in the network through redirected behaviour, even if the initial dyadic encounter was not reciprocated. It can be proposed that the more socially influential sows that are identified in the network will determine how quickly aggression moves through the herd, because as more individuals are reached, ultimately it will lead to the levels of aggression observed.

The socially influential sows are acting as keystone individuals, demonstrated by their higher betweenness centrality than subgroup conspecifics, affording them greater opportunity to broker aggression throughout the herd. Keystone animals are described as 'individuals who have a disproportionately large, irreplaceable effect on group dynamics' (Modlmeier et al., 2014). Identifying group-level keystone individuals is pivotal for implementing strategies to improve welfare and enhance understanding of group dynamics. Keystone animals at group-level have been identified in many species, covering an array of behaviours including, mature female social spiders, *Stegodyphus dumicola*, who act as keystone animals to increase the aggressive foraging of juveniles (Modlmeier et al., 2015), policing pigtailed macaques, *Macaca nemestrina*, that reduce aggression and maintain social cohesion (Flack et al., 2006), adult male sac-winged bats, *Saccopteryx bilineata*, who act as tutors of complex vocalisations skills to pups (Knörnschild et al., 2010), social brokers in bottlenose dolphins, *Tursiops truncatus* (Lusseau and Newman, 2004), policing capuchin monkeys, *Cebus albifrons*, responsible for limiting intra-group conflicts (Berstein,

1966) and key zebrafish, *Danio rerio*, whose removal from the shoal reduces group-foraging success (Vital and Martins, 2011). In contrast to these positive keystone individuals, the introduction of socially unsettling individuals can have a detrimental impact on group dynamics, as seen in yellow baboons, *Papio cynocephalus*, in which just one hyperaggressive male can disrupt social cohesion (Alberts et al., 1992), a characteristic also observed in stream water striders, *Aquarius remigis* (Chang and Sih, 2013). In pigs, a recent study found that compared to low pen-level betweenness centrality, high betweenness centrality 24 hours post mixing predicted an increased risk of chronic aggression three weeks later (Foister et al., 2018). Accordingly, the removal of SIS rather than SPS from an aggression network could serve as an effective measure to reduce the flow and levels of agonistic interactions as individuals with high betweenness centrality can control the exchange of behaviours (Makagon et al., 2012). Stability in the betweenness centrality metrics would also enable more accurate predictions of prospective behaviour than degree centrality, allowing intervention procedures to be applied.

Across all three networks, parity was found to be a significant driver for initiating aggressive behaviour. All parities were shown to be significantly more aggressive than gilts and sows with parity of seven the most aggressive in the herd, demonstrating that this behaviour becomes more prolific with increasing age. The findings are consistent with previous research in which parity, subsequent weight and repeated remixing experience are shown to increase aggressive individual behaviour (Edwards et al., 1994; Arey and Edwards, 1998; Schalk et al., 2018). Additionally, gilts only accounted for a small proportion of the herd in each production cycle, representing 12% of the herd in PC1 (n = 9), 8% in PC2 (n = 6) and 9% in PC3 (n = 7), consequently,

only 2% of all quantified SPS were gilts. By comparison, parity did not impact a notable effect on betweenness centrality above gilt level, as only gilts were found to have significantly lower betweenness centrality than their conspecifics, resulting in fewer gilts quantified as SIS.

Finally, newly mixed sows, individuals introduced into the network during the first week of a production cycle, are significantly less aggressive than resident sows. New sows were also considerably less influential than resident sows based upon betweenness centrality. These findings conflict with previous research that suggests sows will be more aggressive directly after insemination due to the impact of endocrine changes (Stevens et al., 2015). Interestingly, while parity was shown to be a significant contributor to aggressiveness, only 8% of sows remixed during the study period were gilts indicating that the propensity to be aggressive based upon age is context specific.

6.5. Conclusions

The study identified socially prominent and influential sows in all three production cycles, distributed throughout the subgroups. Individuals do not have to be highly connected to be quantified as either socially prominent or influential in aggression networks. Instability in outdegree centrality highlights the complexities of predicting individual aggressive behaviour in a dynamic system. Predictive behaviour is critical for the development of group composition strategies targeted at reducing aggression and improving welfare. The results of this study demonstrate that an individual's innate propensity for aggressive behaviour, whether that be determined by parity or

previous experience is negated by the social context. This finding is crucial as it reveals that dependence upon degree centrality as a metric for determining future behaviour is not the most effective measure as it only provides a snapshot of individual response at any given moment in time. In contrast, the study has found that influence is more relevant to aggression networks, a consequence of reach and the impact of indirect interactions within the herd. Betweenness centrality was found to be a stable trait at an individual level, even when quantifiable social influence was affected by the changing group compositions. The recommendation for future related research is the consideration of betweenness centrality as a more useful predictor of identifying individuals that can impact the flow of and subsequent aggression levels within a dynamic system.

Chapter seven:

The impact of social prominence and influence in three agonistic networks on reproductive performance

7.1. Introduction

Consistency of network position is identified as a highly neglected area of research (Krause et al., 2015). Developing a more detailed understanding of this consistency in a commercial setting would be particularly relevant to welfare and reproduction; few studies have investigated the correlation between network centrality and fitness (McDonald 2007; Ryder et al., 2008; Silk et al., 2009). The direct and indirect mechanisms underpinning the determinant of how being socially central enhances fitness are behaviour dependent. Social centrality in a prosocial network imparts benefits that have a different inherent source to those obtained in an aggression network. Socially prominent individuals that form many prosocial bonds can indirectly improve fecundity and offspring survival (Silk et al., 2003; Cameron et al., 2009; Ramp et al., 2010; Schülke et al., 2010). In comparison, animals that achieve centrality through agonistic interactions gain the direct benefits of access to primary resources and mates, which also indirectly improves overall welfare and reproductive success (King et al., 2011; Surbeck et al., 2012).

Despite the benefits of being socially central in an aggression network, maintaining this form of prominence can be detrimental to the individual. Achieving prominence through agonistic interactions increases the risk of injury and physiological stress that impairs reproduction (Verhulst and Salomons, 2004; Milich et al., 2018). For example, substantial evidence shows aggressive pigs incur higher rates of injuries compared to less aggressive individuals (Turner et al., 2009; Desire et al., 2015; Angarita et al., 2019). Verhulst and Salomons (2004) propose that the fitness consequences of being socially prominent cannot be fully perceived in captive animals due

to an abundance of resources and an absence of the complexities of wild living. Although aggression is the primary weapon for achieving prominence or social stability in numerous species, it is not the despotic behaviour expected in related wild boar groups (Jensen and Wood-Gush, 1984). However, the intensity of pig farming has increased aggression in commercial herds, brought about by enlarged groupings, unfamiliar conspecifics, and remixing to create an unpredictable albeit protected environment. The management practices of implementing dynamic systems with large groupings increases aggression in other commercial species (Andersen et al., 2008; Patullo et al., 2009; Carvalho et al., 2018). The evidence supports a requirement to investigate the fitness consequences of being socially prominent or influential, using pigs as a model species.

The agonistic interactions experienced by commercial pigs during gestation detrimentally affects productivity and piglet development (Tuchscherer et al., 2002; Krandendonk et al., 2006a; Rutherford et al., 2014). A recent review of the procedures already in place to reduce aggression outlines the extent to which it is still a foremost concern with both welfare and economic consequences (Peden et al., 2018). New perspectives of evaluating productivity in the context of temporal social position could provide further insight at an individual level that informs predictions for future productivity. It is already understood that less aggressive pigs are susceptible to challenges that increase social stress affecting production; sustaining higher rates of skin lesions and injuries (Tönepöhl et al., 2013), and increased displacement from enrichment (Elmore et al., 2011). Chapter six found general instability in being socially prominent or influential throughout each production cycle in the aggression networks. The presence of social

inequality in the dynamic herd also implies a disparity in reproductive success and maternal behaviours. Where there is plasticity in social position, it can be hypothesised plasticity will occur in reproductive output due to the positive correlation between social stressors and production measures outlined in previous research. With the application of social network analysis, this study will investigate the relationship between being either socially prominent or influential, based upon individual aggressiveness, and productivity. The study will analyse the effects of these traits on prepartum, preweaning piglet mortality and sow maternal behaviour. The research will evaluate the inter and intra-individual variation in production metrics across three production cycles and assess the effect of parity on these measures.

7.2. Methods

A detailed description of animals, housing and social network properties are described in chapter two. A brief description follows.

7.2.1. Animals and housing

The study was conducted at Sturgeons farm, Writtle University College, Chelmsford, Essex between November 2017, and January 2018. Sturgeons farm supports an eighty-sow unit, and the study herd consisted of a commercial cross of Large White-Landrace and Pietrain breeds, parities one to seven, housed in a dry sow barn. Sows were fed on a complete feed for breeding sows through electronic sow feeders, reset daily at 15:00 h, with additional *ad libitum* access to straw. Sturgeons farm operates a dynamic system in which small groups of sows are remixed into the

herd every third Tuesday. There is a repeated cycle of production following the pattern, farrowing week, breeding week, and weaning week. For individual identification, each sow was marked with coloured dots, stripes, or both on their backs. Colour codes corresponded to ear-tag number.

7.2.2. Data collection

7.2.2.1. Sow reproduction data

Access to the farm diaries and liaising with the pig unit manager provided relevant information concerning parity, farrowing date, insemination date and date of remixing. The diaries also provided all data concerning reproduction including live-born piglets, stillborn piglets, mummified foetuses, and any cause of piglet mortality following birth until weaning including hypothermia, starvation, scours, crushing, lameness, low viability, and unknown causes of preweaning death (Chapter 5, Table 10) Associations between production and social network metrics were investigated, data were taken from the farrowing event that occurred directly after a sow had been removed from any of the three production cycles. To examine the stability of reproductive performance, data were also taken from the farrowing event that followed the first. Data for the second farrowing event was not available for every sow observed during the three production cycles due to culling or a second farrowing event had yet to occur before analysis.

7.2.2.2. Video observation data

A total of five CCTV H.265 4 Mega Pixel Eyeball PoE, infrared dome cameras were installed in the dry barn to capture and observe sow behaviour. Each camera was positioned to provide unobstructed, direct visual access to all essential functional areas (Chapter two, Figure 3). The

areas included the straw bedded area, the passageway, the ESF area, and the nipple-drinkers. Three hours per day were selected for observation, proven to be the optimum periods when the sows were most active, 08:00-09:00 h, 15:00-16:00 h and 20:00-21:00 h. Observations occurred over three 21-day production cycles from 20th November 2017 until 21st January 2018. The video observations occurred on seven preselected days of each production cycle, including the day before remixing (day 20) and the day of mixing (day 21). The observations continued, on the three consecutive days that followed a mixing event (days 1,2,3). Days 7 and 14, following remixing, were also selected. Overall, the study included 21 h of video footage for each production cycle providing 63 h of behaviours for analysis.

7.2.2.3. Social behaviours

The behaviour sampling method used an all-occurrences method of observation, considered the most effective and appropriate form of direct sampling method for observing rarer behaviours such as aggression (Martin and Bateman, 2007). The method is consistent with current, related research (i.e., Foris et al., 2018). Every occurrence of agonistic interactions (Chapter six, Table 16) was documented during the predetermined periods in PC1, PC2 and PC3. Behavioural observations recorded who attacked whom and if these interactions were reciprocated, allowing for the construction of directed networks. The frequency of agonistic interactions was recorded to allow for a weighted representation of the three production cycles. No threshold measures were applied to the network, consistent with other social network analysis of aggression (i.e., Büttner et al., 2015) and all three production cycles reflect the original network compositions.

7.2.3. Network construction

7.2.3.1. Identification of subgroups

K-cores have been applied to each aggression network in the production cycles to ascertain subgroups based upon connectedness. A *k*-core is a subgraph in which every node has degree *k* or more connections with other nodes within the subgraph (Borgatti et al., 2018).

7.2.3.2. Quantifying social prominence in the agonistic networks

Degree centrality can provide a measure of prominence within subgroups (Gero et al., 2013). Prominent animals with a significantly higher degree centrality than their conspecifics are consequently more highly connected (Verdolin et al., 2014). Within the agonistic networks in the three production cycles, sows with an outdegree centrality above the 95% range of outdegree centralities for their *k*-core subgroup quantified as socially prominent (adapted from Verdolin et al., 2014). Hereafter, quantified sows are referred to as socially prominent sows (SPS) and sows' not quantified SPS are referred to as non-SPS.

7.2.3.3. Quantifying social Influence in the agonistic networks

Betweenness centrality can provide a measure of influence within and between subgroups (Lusseau and Newman, 2004). Individuals with a significantly higher betweenness centrality than their conspecifics are subsequently more influential. Within the agonistic networks in the three production cycles, sows with a betweenness centrality above the 95% confidence range of the betweenness centralities for their *k*-core subgroup quantified as socially influential (adapted from Verdolin et al., 2014). Hereafter, socially influential sows will be referred to as SIS and a sow not quantified as socially influential will be referred to as non-SIS.

7.2.3.4. The coefficient for quantifying SPS and SIS in the agonistic networks

Socially prominent and influential sows either identified as those individuals whose outdegree centrality or betweenness centrality or both fell above the 95% confidence interval range for their assigned subgroup (*k*-core). This method is consistent with previous social network research (i.e., Verdolin et al., 2014). These individuals quantified applying the following coefficient, $x \pm z * s/ \sqrt{n}$. Where:

x = Mean outdegree centrality or the betweenness centrality for the *k*-core

z = 1.96, for the 95% confidence interval

s = Standard deviation of the outdegree centrality or the betweenness centrality for the *k*-core

$\sqrt{n}$ = Square root of the *k*-core population total

7.2.4. Data analysis

Matrices of the aggression networks for each production cycle were constructed in Excel and imported into Ucinet 6, version 6.634 (Borgatti et al., 2002). The general network and individual network metrics analysed in Ucinet included degree centrality and betweenness centrality. Statistical analysis was performed in R.3.4.1 (R Development Core Team, 2017). Data was subsequently tested for normality via histograms and the Shapiro Wilks test. The data were found to be nonnormally distributed. GLMMs were performed in R.3.4.1 (R Development Core Team, 2017) using the R package lme4, version 1.1-21 (Bates et al., 2015) to test for differences in production metrics between quantified and non-quantified sows. Additional testing was also conducted to investigate differences in production metrics over two farrowing events. The multiple GLMMs were corrected to reduce the risk of type 1 errors with the application of the

false discovery rate (FDR). Upon testing, the negative binomial model was found to be the best fit for the probability distribution. For each model, the pig identification number represented the random effects, and fixed effects included farrowing event and social role. Associations between the centrality metrics (outdegree centrality and betweenness centrality) and production metrics were performed using the Spearman's rank correlation coefficient using the R package corrplot, version 0.84 (Wei and Simko, 2017).

7.3. Results

7.3.1. The identification of socially prominent sows

Please refer to Table 18 in Chapter six that provides a detailed description of the socially prominent sows identified within the subgroups of PC1, PC2 and PC3. PC1 quantified 21 SPS, PC2 quantified 17 SPS and PC3 quantified 16 SPS. Table 18 shows the number of individuals, not specific individuals. Outdegree centrality data is weighted to account for times when sows were absent from a network.

7.3.2. Production metrics and social prominence

Table 20. The mean frequency ± SD for liveborn, prenatal and postpartum piglet mortality rates for socially prominent sows (SPS) and sows not prominent (non-SPS) in production cycle 1, production cycle 2 and production cycle 3. Data were taken from farrowing events occurring directly after being in an aggression network between November 2017 and January 2018 at Sturgeons Farm, Essex. PC = Production cycle. SPS = Socially prominent sow. Non-SPS = A sow not quantified as socially prominent. SD = Standard deviation

Production metric	Production cycle 1 Mean frequency ± SD	Production cycle 2 Mean frequency ± SD	Production cycle 3 Mean frequency ± SD
Live-born	SPS: 12.1 ± 3.3 Non-SPS: 12.1 ± 4.0	SPS: 11.8 ± 3.2 Non-SPS: 12.5 ± 3.3	SPS: 12.6 ± 3.3 Non-SPS: 12.5 ± 3.5
Stillborn	SPS: 1.4 ± 1.8 Non-SPS: 1.7 ± 3.1	SPS: 1.7 ± 1.9 Non-SPS: 1.7 ± 3.0	SPS: 1.9 ± 2.1 Non-SPS: 2.0 ± 3.1
Mummified foetuses	SPS: 0.1 ± 0.5 Non-SPS: 0.2 ± 0.6	SPS: N/A Non-SPS: 0.2 ± 0.6	SPS: 0.1 ± 0.3 Non-SPS: 0.1 ± 0.4
Total prenatal mortality	SPS: 1.5 ± 1.9 Non-SPS: 2.1 ± 3.3	SPS: 1.7 ± 1.9 Non-SPS: 1.9 ± 3.2	SPS: 1.9 ± 1.9 Non-SPS: 2.1 ± 3.2
Low viability	SPS: 0.4 ± 0.7 Non-SPS: 0.9 ± 1.4	SPS: 0.6 ± 1.4 Non-SPS: 0.7 ± 1.1	SPS: 0.5 ± 1.4 Non-SPS: 0.9 ± 1.3
Crushed	SPS: 0.4 ± 0.7 Non-SPS: 0.7 ± 1.1	SPS: 0.6 ± 1.3 Non-SPS: 0.6 ± 0.9	SPS: 0.6 ± 1.0 Non-SPS: 0.7 ± 1.3
Total postpartum mortality	SPS: 1.9 ± 1.7 Non-SPS: 2.1 ± 2.5	SPS: 2.1 ± 3.0 Non-SPS: 1.7 ± 1.9	SPS: 1.4 ± 2.5 Non-SPS: 1.4 ± 1.9
Total piglet mortality	SPS: 3.3 ± 2.5 Non-SPS: 3.9 ± 3.7	SPS: 3.8 ± 3.3 Non-SPS: 3.6 ± 3.5	SPS: 3.1 ± 3.2 Non-SPS: 3.6 ± 3.7

7.3.3. The relationship between outdegree centrality and production metrics

The network centrality metrics of all three production cycles were combined to investigate an overall association between outdegree centrality and reproductive performance. Associations do not account for whether an individual is quantified SPS, instead refers only to the data pertaining to outdegree centrality. Associations include every individual in all three production cycles, where production data was available (n=228).

7.3.3.1. Outdegree centrality and live-born piglets

No association was found between outdegree centrality and the frequency of live-born piglets, r_s = -0.0096, p = 0.89. Live-born numbers remained consistent over all three networks for SPS and non-SPS (Table 20).

7.3.3.2. Outdegree centrality and prenatal piglet mortality

No association was found between outdegree centrality and stillborn piglets, r_s = 0.043, p = 0.52, with no significant differences between SPS and non-SPS in any of the production cycles, coef. -0.06, z -0.283, p = 0.78. There was also no association between outdegree centrality and mummified foetuses, r_s = 0.038, p = 0.57 or significant differences in numbers of mummified piglets between SPS and non-SPS in all three production cycles, coef. -0.56, z -0.746, p = 0.46. At an individual level, when all sows were categorised as either sow with stillborn piglets or those without, there were no significant differences in outdegree centrality (coef. -0.11, z -0.647, p = 0.52). Results indicate that initiating aggression does not have a significant effect on prepartum piglet mortality.

7.3.3.3. Outdegree centrality and postpartum piglet mortality

No association was found between outdegree centrality and low viability piglets in any of the production cycles, r_s = -0.038, p = 0.57 or significant differences in numbers of low viability piglets between SPS and non-SPS, coef. -0.26, z -0.914, p = 0.36. There was no association between outdegree and crushing behaviour, r_s = 0.097, p = 0.15 or significant differences in crushing behaviour between SPS and non-SPS, coef. -0.37, z -1.407, p = 0.16. Initiated aggression was

revealed to have no impact upon starvation, hypothermia, lameness, or scours. When all sows were categorised as either crushers or non-crushers, there were no significant differences in outdegree centrality (coef. 0.11, z 0.611, p = 0.54). Results indicate that initiating aggression does not have a significant effect on postpartum piglet mortality.

7.3.3.4. Social prominence and the stability of production metrics over two farrowing events

Table 21. The mean frequency ± SD for stillbirths, mummified piglets, low viability piglets and crushed piglets for SPS quantified at least twice (n=13), SPS quantified only once (n=17) and non-SPS (n=53) over the three production cycles. Data were taken from two farrowing events for each sow. The first farrowing event occurred directly after sows were removed from any of the three production cycles. The second farrowing event followed the first. There were significant changes in stillbirths over two farrowing events (coef. 0.62, z 2.486, $p < 0.05$: $p = 0.0129$). for non-SPS and significant changes in mummified piglets, coef. -1.32, z -2.338, $p<0.05$: $p = 0.0194$. All other metrics remained stable for all classified sows. SPS twice = sows were quantified prominent at least twice. SPS once = sows were only quantified prominent once. Non-SPS = sows were never quantified prominent. SD = standard deviation.

Production metric	**Farrowing Event 1 Mean frequency ± SD**		**Farrowing Event 2 Mean frequency ± SD**	
Stillborn	SPS Twice:	1.8 ± 2.2	SPS Twice:	2.1 ± 1.5
	SPS Once:	1.2 ± 1.3	SPS Once:	2.5 ± 2.4
	Non-SPS:	**1.1 ± 2.6 ***	**Non-SPS:**	**1.9 ± 2.5 ***
Mummified	SPS Twice:	0.4 ± 0.7	SPS Twice:	N/A
	SPS Once:	0.1 ± 0.3	SPS Once:	N/A
	Non-SPS:	**0.3 ± 0.7***	**Non-SPS:**	**0.1 ± 0.3***
Low viability	SPS Twice:	0.9 ± 1.3	SPS Twice:	0.4 ± 1.3
	SPS Once:	0.9 ± 1.4	SPS Once:	1.2 ± 2.1
	Non-SPS:	0.6 ± 1.0	Non-SPS:	0.6 ± 1.2
Crushed	SPS Twice:	N/A	SPS Twice:	1.0 ± 2.0
	SPS Once:	0.7 ± 1.0	SPS Once:	1.4 ± 2.1
	Non-SPS:	0.5 ± 0.8	Non-SPS:	0.5 ± 0.8

***$p<0.05$**

7.3.4. The identification of socially influential sows

Please refer to Table 19 in Chapter six that provides a detailed description of the socially influential sows identified within the subgroups of PC1, PC2 and PC3. PC1 quantified 23 SIS, PC2 quantified 20 SIS and PC3 quantified 22 SIS. Table 19 shows the number of individuals, not specific individuals. Betweenness centrality data is weighted to account for times when sows were absent from a network.

7.3.5. Production metrics and social influence

Table 22. The mean frequency ± SD for liveborn, prenatal and postpartum piglet mortality rates for socially influential sows (SIS) and sows not influential (non-SIS) in production cycle 1, production cycle 2 and production cycle 3. Data were taken from farrowing events occurring directly after being in an aggression network between November 2017 and January 2018 at Sturgeons Farm, Essex. SIS = Socially influential sow. Non-SIS = A sow not quantified as socially influential. SD = Standard deviation. PC = Production cycle.

Production Category	PC1 Mean frequency ± SD	PC2 Mean frequency ±	PC3 Mean frequency ± SD
Live-born	SIS: 12.1 ± 4.2 Non-SIS: 12.1 ± 3.7	SIS: 11.9 ± 3.6 Non-SIS: 12.5 ± 3.1	SIS: 12 ± 3.9 Non-SIS: 12.8 ± 3.3
Stillborn	SIS: 1.2 ± 1.7 Non-SIS: 1.8 ± 3.2	SIS: 2.1 ± 3.1 Non-SIS: 1.6 ± 2.7	SIS: 1.6 ± 1.6 Non-SIS: 2.2 ± 3.3
Mummified foetuses	SIS: 0.2 ± 0.6 Non-SIS: 0.2 ± 0.6	SIS: 0.2 ± 0.7 Non-SIS: 0.2 ± 0.5	SIS: 0.1 ± 0.4 Non-SIS: 0.1 ± 0.4
Total prenatal mortality	SIS: 1.4 ± 1.8 Non-SIS: 2.1 ± 3.3	SIS: 2.3 ± 3.4 Non-SIS: 1.7 ± 2.8	SIS: 1.7 ± 1.7 Non-SIS: 2.3 ± 3.4
Low viability	SIS: 0.7 ± 1.2 Non-SIS: 0.8 ± 1.3	SIS: 0.5 ± 1.2 Non-SIS: 0.7 ± 1.1	SIS: 0.6 ± 1.3 Non-SIS: 0.9 ± 1.4
Crushed	SIS: 0.7 ± 1.1 Non-SIS: 0.6 ± 0.9	SIS: 0.8 ± 1.2 Non-SIS: 0.5 ± 0.9	SIS: 0.4 ± 0.8 Non-SIS: 0.8 ± 1.4
Total postpartum mortality	SIS: 2.3 ± 2.6 Non-SIS: 1.9 ± 2.2	SIS: 1.7 ± 2.6 Non-SIS: 1.8 ± 2	SIS: 1.2 ± 2.0 Non-SIS: 1.4 ± 2.1
Total piglet mortality	SIS: 3.9 ± 3.1 Non-SIS: 3.7 ± 3.5	SIS: 4.0 ± 4.1 Non-SIS: 3.5 ± 3.2	SIS: 3.0 ± 3.0 Non-SIS: 3.8 ± 3.8

7.3.6. The relationship between betweenness centrality and production metrics

The network centrality metrics of all three production cycles were combined to investigate an overall association between betweenness centrality and reproductive performance. Associations do not account for whether an individual is quantified SIS, instead refers only to the data pertaining to betweenness centrality. Associations include every individual in all three production cycles, where production data was available (n=228).

7.3.6.1. Betweenness centrality and live-born piglets

No association was found between live-born piglet numbers and betweenness centrality, r_s = 0.00051, p = 0.99. Live-born numbers remained consistent over all three production cycles for SIS and non-SIS (Table 22).

7.3.6.2. Betweenness centrality and prenatal piglet mortality

No association was found between stillborn piglets and betweenness centrality, r_s = -0.031, p =0.65, with no significant differences between SIS and non-SIS, coef. -0.03, z -0.214, p = 0.83. There was also no association between mummified foetuses and betweenness centrality, r_s = 0.073, p = 0.27, with no significant differences between SIS and non-SIS, coef. 0.07, z 0.172, p = 0.86. At an individual level, when sows were categorised as those with stillborn piglets and those without, there were no significant differences in betweenness centrality (coef. -0.01, z -0.075, p = 0.94). Results indicate that being socially influential in an aggression network does not significantly affect prenatal piglet mortality.

7.3.6.3. Betweenness centrality and postpartum piglet mortality

No association was found between low viability piglets and betweenness centrality, r_s = -0.026, p = 0.7, with no significant differences between SIS and non-SIS, coef. -0.16, z -0.611, p = 0.54. There was also no association between crushing behaviour and betweenness centrality, r_s = 0.098, p = 0.14, no significant differences between SIS and non -SIS, coef. -0.24, z -0.938, p = 0.35. No impact of betweenness centrality was found on starvation, hypothermia, lameness, or scours. At an individual level, when sows were categorised as either crushers or non-crushers, there were no

significant differences in betweenness centrality (coef. -0.102, z -0.639, p = 0.52). Results indicate that being socially influential in an aggression network does not significantly affect postpartum piglet mortality.

7.3.6.4. Social influence and the stability of production metrics over two farrowing events

Table 23. The mean frequency ± SD for stillbirths, mummified piglets, low viability piglets and crushed piglets for SIS quantified at least twice (n= 13), SIS quantified only once (n=31) and non-SIS (n=40) over the three production cycles. Data were taken from two farrowing events for each sow. The first farrowing event occurred directly after sows were removed from any of the three production cycles. The second farrowing event followed the first. There were significant changes in crushing behaviour over two farrowing events (coef. -1.10, z 2.486, $p < 0.05$: $p = 0.0129$) for SIS quantified at least twice. SIS quantified only once showed significant differences in rates of mummified piglets over two farrowing events, coef. -2.70, z -2.607, $p < 0.01$, $p = 0.00912$. Non-SIS showed significant differences in stillborn rates over two farrowing events, coef. 0.74, z 2.633, $p < 0.01$, $p = 0.00846$ and low viability piglets, coef. -0.33, z -55.88, $p < 0.001$. All other metrics remained stable for all classified sows. SIS twice = sows were quantified influential at least twice. SIS once = sows were only quantified influential once. Non-SIS = sows were never quantified influential. SD = standard deviation.

Production metric	**Farrowing Event 1 Mean frequency ± SD**		**Farrowing Event 2 Mean frequency ± SD**	
Stillborn	SIS Twice:	0.9 ± 1.8	SIS Twice:	2.1 ± 1.7
	SIS Once:	1.6 ± 1.6	SIS Once:	1.8 ± 2.5
	Non-SIS:	**1.2 ± 2.8***	**Non-SIS:**	**2.2 ± 2.4***
Mummified	SIS Twice:	N/A	SIS Twice:	N/A
	SIS Once:	**0.5 ± 0.9***	**SIS Once:**	**0.04 ± 0.2***
	Non-SIS:	0.2 ± 0.5	Non-SIS:	0.1 ± 0.3
Low viability	SIS Twice:	0.5 ± 1.2	SIS Twice:	0.8 ± 1.5
	SIS Once:	0.5 ± 0.6	SIS Once:	0.6 ± 1.1
	Non-SIS:	**0.9 ± 1.4***	**Non-SIS:**	**0.7 ± 1.6***
Crushed	**SIS Twice:**	**1.3 ± 1.1***	**SIS Twice:**	**0.4 ± 1.1***
	SIS Once:	0.5 ± 0.9	SIS Once:	0.9 ± 1.6
	Non-SIS:	0.5 ± 0.7	Non-SIS:	0.8 ± 1.4

***p<0.05**

7.4. Discussion

This study has revealed when a snapshot of behaviour is observed in any given production cycle, being socially prominent or influential in the aggression networks of a dynamic sow herd does not impact production metrics. There was no association found between outdegree centrality or

betweenness centrality or any production metrics; with no significant differences in live-born piglets, prenatal or postpartum piglet mortality between significantly more aggressive sows and those found to be more passive. Previous research has extensively focussed on the effects of aggression on the recipient; including higher injury rates and weight loss (Krandendonk et al., 2007), increased piglet mortality (Rutherford et al., 2014) and detrimental effects on piglet growth, and development (Tuchscherer et al., 2002; Krandendonk et al., 2006b; Rault et al., 2013). In contrast, the perspective of this study focussed on the initiator of aggression by analysing only outdegree centrality. Although being aggressive may present certain benefits in a large social group, it appears these benefits do not extend to enhanced reproductive performance or piglet survival in a commercial herd. A finding consistent with previous research in other commercial species; in which unstable social environments increase aggression but do not ultimately impact on reproduction (Andersen et al., 2008). Regardless of whether a sow quantified as SPS, non-SPS, SIS or non-SIS, the levels of individual aggressiveness did not affect reproductive performance.

It is expected that a reproductive skew might occur within what is fundamentally a despotic society (Tombak et al., 2019), in which those that are socially prominent or influential should engender an environment where these individuals gain enhanced fitness. In a recent study, dominant hens produced higher numbers and heavier eggs than their subordinates (Carvalho et al., 2018). Despotic societies are dependent on the few dominant individuals that ‘rule’, however, substantial variance in centralisation between production cycles and instability in social prominence (shown in Chapter six) indicate that without consistency in a social role the potential for reproductive success would become more evenly distributed. This behavioural variance

presents an explanation for the findings. The previous chapter outlined the instability of aggressive behaviour, suggesting context-dependent reactions are determined by individual-level decision making in response to changes in the social herd. This individuality could also account for the lack of differences in the production metrics between quantified and non-quantified sows. Contrasting in the belief that environmental or social challenges will compromise reproduction and maternal behaviour, research is beginning to suggest that individual coping strategies and behavioural characteristics can negate social stressors (O'Malley et al., 2019). Turner et al*.,* (2005) suggest, accounting for individual behavioural variance, that for reproductive processes to be impaired in a proportion of pigs, stress must be prolonged or sustained. It is at this level of evaluation that patterns begin to emerge from the current study. A snapshot of performance from one farrowing event indicated no significant differences in reproductive performance between quantified and non-quantified sows. However, when accounting for two farrowing events, differences were revealed. Sows not quantified SPS or SIS over all three production cycles performed significantly differently over two farrowing events, compared to animals quantified once or twice. There was a discrepancy in the results for SIS quantified twice, in which SIS quantified twice presented a larger numerical difference between farrowing events than non-SIS but was found not to be significant. It is likely that the results for SIS twice are indicative of the low number of sows in this category (n = 13), as sample size can impact upon tests of effect (Charan and Kantharia, 2013).

Within the social prominence categories, only non-SPS demonstrated instability in reproductive performance, with a significant increase in the numbers of stillborn piglets and a significant

decrease in mummified piglets between the first, and second farrowing event. Sows quantified socially prominent only once or twice reflected more stable reproductive performance with no significant differences in stillbirths, mummifications, low viability piglets or crushing behaviour over two farrowing events. The findings are consistent with recent research that documented the concept of a carry-over effect of aggression between parities. Lagoda et al., 2021 found that sows with high skin lesions due to mixing aggression in one parity had an increase rate of piglet mortality during the second parity. In the social influence categories, production instability was also found in sows never quantified as socially influential, again with a significant increase in stillbirths over two farrowing events and a decrease in the numbers of low viability piglets. Interestingly, social influence led to instability in the mummified piglet rates of SIS quantified only once and a considerable reduction in the crushing behaviour of SIS quantified at least twice. Despite the lack of association between the centrality metrics and production metrics, the findings over two farrowing events suggest that continuing to be non-SPS or non-SIS impairs reproduction concerning stillborn piglet numbers. However, the lack of centrality metrics for the second farrowing event presents a caveat as it is likely that centrality metrics prior to the second farrowing event may be a more relevant proximate cause of reproductive traits than centrality metrics taken before the first farrowing.

Stillbirths are identified in both the preferential association and aggression networks as the production metric most impacted upon by prolonged individual reactivity to the social environment. Although this study is unable to identify the direct causation of how the underlying biological mechanisms are affected, the likelihood is that being more aggressive may impart

benefits such as enhanced access to desirable resources, which may have positive effects on the neuroendocrine system. It might also be expected that if an individual repeatedly engages in any form of agonistic encounter, whether it is initiating or receiving, that would be detrimental to reproductive performance. Yet, this study demonstrates that continuing to initiate significantly more aggression during a production cycle stabilises reproductive performance. One possible explanation for this anomaly is succinctly described by Kelly and Wilson (2020). They proposed that *'aggression and prosocial behaviour may be two sides of the same coin, operating along a sliding scale of mechanistic continuum*' (p3). Concerning reproductive performance, this can be interpreted as the similar outcomes of being repeatedly quantified either SPS or SIS in both the preferential association and aggression networks, despite fundamental differences to the origins where productivity is affected. Social bonding and affiliative behaviour, such as in the preferential association networks increases levels of the neuropeptide oxytocin (Ross and Young, 2009), also reducing cortisol production (Wittig et al., 2016). Behaviours motivated by aggression mediate the steroid hormone progesterone (Davis and Marler, 2003), an influencing factor in porcine stillbirths (Liu et al., 2020). Despite the complexities associated with the hormonal impact of social behaviour on reproduction, it seems that individual stability in the initiation of significantly high levels of aggressiveness in gestating sows may be less costly 'reproductively speaking' than not being socially prominent at all in a dynamic aggression network.

7.5. Conclusions

The most important finding of this study is identifying the need to extend beyond a single farrowing event to ascertain any long-term effects of social influence or prominence on

reproductive performance. When accounting for only a single farrowing event, no association was found between outdegree centrality, betweenness centrality and any of the production metrics. Over two farrowing events, however, revealed sows who never quantified SPS or SIS in any of the production cycles had an increase in stillbirth numbers in the second farrowing event. The findings suggest there are long-term reproductive benefits to being significantly more aggressive in a dynamic sow herd, although the source of this positive effect is presently unclear. Identifying that social prominence or influence may be a tool to stabilise productivity, allowing for predictions of reproductive performance at an individual level.

Chapter 8

The structure and temporal changes of brokerage roles over two dynamic production cycles of dry breeding sows

8.1. Introduction

'*Describing the social structure of a species is the first step toward understanding its social organisation*' (Wells et al., 1987). Traditional methods of dyadic observations between conspecifics provide some insight into the social mechanisms of gregarious species. Nevertheless, dyadic interactions do not account for the essential elements of indirect interactions (Sih et al., 2009, Wey and Blumstein, 2010; Brent, 2015), failing to fully explain the complexities of social behaviour in the context of the whole network. These complexities refer to the multitude of positive and negative social interactions through which sociality can occur. Socio-positive indirect interactions enhance fitness, welfare, and wellbeing through the ability to acquire and transfer information. Also, engendering resource allocation knowledge (Schakner and Blumstein, 2016), the acquisition of valuable skills (Aplin et al., 2013) and social bonding. Indirect socio-negative interactions play a role in the social transmission of undesirable behaviours (Zeltner et al., 2000) and the transference of redirected aggression (Tokuyama and Furuichi, 2014).

Animal research has demonstrated that identifying influential and highly connected individuals within a social group is a salient tool for understanding social dynamics (Lusseau and Newman, 2004; Verdolin et al., 2014). The findings of indirect interaction studies do, however, suggest that every individual in a social group has the potential to play a role in the construction of a social network, regardless of their social standing. Individual differences in their ability to engage in an indirect interaction have been documented in non-domestic animal research. A study of captive chimpanzees (*Pan troglodytes*) found highly sociable individuals were not influential in

establishing links between unconnected conspecifics (Kanngiesser et al., 2011). Similarly, indirect lekking interactions, rather than direct interactions, in long tailed manakins (*Chiroxiphia linearis*) proved an accurate predictor of future social status (McDonald, 2007). Mann et al. (2012) found that 'sponging' bottlenose dolphins (*Tursiops truncates*) demonstrated a greater ability for cultural learning than individuals more highly connected through direct interactions.

This understanding of the significance and power of indirect interactions in network construction and the role of individuality presents a unique opportunity to investigate welfare issues, particularly those longstanding issues associated with captive living. One major area of welfare and economic concern in which optimum management strategies have not been established is the prevalence of agonistic behaviours in commercial pig herds (Greenwood et al., 2014, Peden et al., 2018). The abolishment of sow stalls in 2013 (EU Council Directive, 2008) has led to an increase in dynamic group housing systems. It is well established that acute aggression occurs directly after mixing within dynamic sow systems, a result of the innate need of animals to reform social hierarchy (Turner et al., 2017). Conversely, how the control and flow of aggression indirectly moves through a network over time, at an individual level, is not fully represented in the literature. For example, Verdon et al. (2018) highlight the difficulties of predicting aggressive behaviours over contexts due to social complexities. The ability, therefore, to identify how pigs indirectly control the flow of aggression in a network could provide valuable insight.

In recent years there has been a rise in the application of social network analysis (SNA) in animal behavioural studies enabling extension beyond the limitations of dyadic interactions to investigate

indirect interactions. The SNA mechanism for identifying transmission of behaviour, information, or disease through indirect interactions between individuals is referred to as social brokerage. By bridging the gap between unconnected individuals, within and between subgroups, brokers are filling the structural holes of a network (Burt, 2001). Thus, enabling the transfer of a specified behaviour or cognitive process, such as aggression. Understanding how aggression flows through a network extends beyond the basic principles of social brokerage, i.e., merely bridging a gap between unconnected individuals. A result of considering the complexities of behavioural interactions and group affiliations that may be influenced by a specific or dominant brokerage role. In human studies, this level of analysis is performed with the application of brokerage typology (Gould and Fernandez, 1989), in which specific brokerage roles can be identified. These roles include those of coordinator, representative, gatekeeper, liaison, and consultant (Chaudhary and Warner, 2015). The significance of identifying specific types of brokerage role is that it enables characterisation of a network either socially, economically, or politically. For example, Fernandez and Gould (1994) demonstrated that the type of brokerage role determined influence and power within the setting of the US health organisation's communication network. They revealed that representatives were the most influential communicators; liaisons and consultants were only influential when communicating with impartial parties.

Whereas no animal studies have applied brokerage typology; specific roles can be inferred through previous behavioural research. An example is demonstrated in captive rhesus macaques (*Macaca mulatta*) where specific individuals control and monitor the levels of aggression through policing behaviour (McCowan et al., 2018). These policing macaques are in effect, coordinating

with their conspecifics to reduce aggression. A network dominated by policing macaques would accordingly be more stable (Beisner et al., 2019). Specific roles can additionally be inferred in heterospecific interactions, shown in a study of wild mixed-species tits (Paridae). Marsh tits (*Poecile palustris*) proved to be key stone individuals because of their ability to act as liaisons between blue tits (*Cyanistes caerulus*), and great tits (*Parus major*) enabling the dissemination of information about foraging sites during winter across species (Farine et al., 2015b). The emergence of applying brokerage typology reveals a powerful tool in further understanding social network structure and characterisation (Fernandez and Gould, 1994; Bellotti, 2009). While animal studies have identified keystone and influential individuals, none have characterised social networks based on brokerage typology. This study will first apply brokerage typology to two aggression networks of a dynamic sow herd to investigate distinct brokerage roles in the network construction and flow of agonistic behaviours. The second aim will characterise the structure of two dynamic networks based upon brokerage typology to determine the effect of brokerage role on an individual's ability to transfer aggression through the herd. The third objective will look at the consistency of an individual to assume a specific role over two production cycles to establish if roles are stable or temporal.

8.2. Methods

A detailed description of the general methods is outlined in Chapter two. A brief description follows.

8.2.1. Animals and housing

The study was conducted at Sturgeons farm, Writtle University College, Chelmsford, Essex between November 2017, and December 2017. Sturgeons farm supports an eighty-sow unit, and the study herd consisted of a commercial cross of Large White-Landrace and Pietrain breeds, parities one to seven, housed in a dry sow barn. Sows were fed on a complete feed for breeding sows through electronic sow feeders, reset daily at 15:00 h, with additional *ad libitum* access to straw. Sturgeons farm operates a dynamic system in which small groups of sows are remixed into the herd every third Tuesday. There is a repeated cycle of production following the pattern, farrowing week, breeding week, and weaning week. For individual identification, each sow was marked with coloured dots, stripes, or both on their backs. Colour codes corresponded to ear-tag number.

8.2.2. Data collection

8.2.2.1. Sow data

Access to the farm diaries and liaising with the pig farm manager provided relevant information concerning parity and date of remixing.

8.2.2.2. Video observation data

A total of five CCTV H.265 4 Mega Pixel Eyeball PoE, infrared dome cameras were installed in the dry barn to capture and observe sow behaviour. Each camera was positioned to provide unobstructed, direct visual access to all essential functional areas (Chapter two, Figure 3). The areas included the straw bedded area, the passageway, the ESF area, and the nipple-drinkers.

Three hours per day were selected for observation, proven to be the optimum periods when the sows were most active, 08:00-09:00 h, 15:00-16:00 h and 20:00-21:00 h. Observations occurred over two 21-day production cycles from 20th November until 31st December 2017. The video observations occurred on seven preselected days of each production cycle, including the day before remixing (day 20) and the day of remixing (day 21). The three consecutive days that followed remixing (days 1,2,3) and days 7 and 14 were also selected. Overall, the study included 21 h of video footage for each production cycle providing 42 h of behaviours for analysis.

8.2.2.3. Social behaviours

All occurrences of agonistic behaviours (Chapter six, Table 16) in PC1 and PC2 were captured using video observations during the predetermined periods. Behavioural observations recorded who attacked whom and if these interactions were reciprocated, allowing for the construction of directed networks. The frequency of aggression was recorded to allow for a weighted representation of the two production cycles. No threshold measures were applied to the network, consistent with other social network analysis of aggression (i.e., Büttner et al., 2015) and both production cycles reflect the original network compositions.

8.2.3. Network construction

8.2.3.1. Identification of subgroups

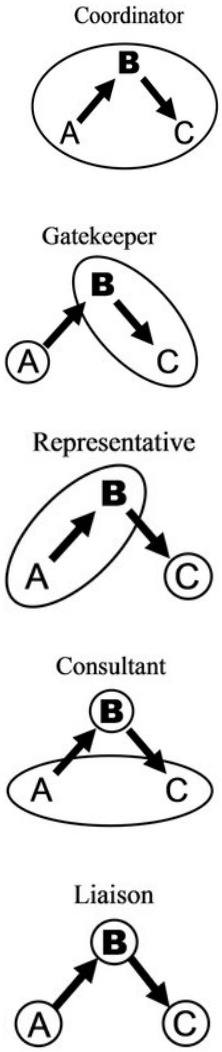
K-cores have been applied to the agonistic networks in PC1 and PC2 to ascertain subgroups based upon connectedness. A *k*-core is a subgraph in which every node has degree *k* or more connections with other nodes within the subgraph (Borgatti et al., 2018).

8.2.3.2. Visualisation of the networks

Visualisation of the social networks for agonistic interactions between specific brokerage roles in PC1 and PC2 were shown as sociograms. The networks consist of directed ties, in which the initiator and recipient of the interaction are displayed, allowing for the visualisation of 'who attacked whom'. Although edges are not weighted in the sociograms, all networks recorded the frequency of indegree centrality (received ties) and outdegree centrality (initiated ties).

8.2.3.3. Applying brokerage typologies

Brokerage position (Burt, 1992; Fernandez and Gould, 1989) is a measure of the extent to which individuals lie on the directed path between two unconnected nodes, thereby acting as a bridge. Brokerage typology (Figure 18) consists of five potential brokerage roles, coordinator, consultant, gatekeeper, representative and liaison (Chaudhary and Warner, 2015). To investigate differences in the brokerage roles within the network, and how aggression is brokered, census data and normalised relative brokerage scores (raw scores divided by the expected value) were applied to the directed aggression data for PC1 and PC2. These scores produce a brokerage profile for every individual within the network, showing the extent to which individuals have engaged in a specific brokerage role. For the analysis, subgroups were applied to every individual with the construction of an attribute file in Ucinet. The subgroups refer to the *k*-cores, a measure of individual connectedness.



Coordinators (**B**) broker between unconnected individuals (A & C) of the same subgroup (Fernandez and Gould, 1994, Gould and Fernandez, 1989).

Gatekeepers (**B**) broker between unconnected individuals, one within the same subgroup (C) as the gatekeeper and one belonging to a different subgroup (A) (Fernandez and Gould, 1994, Gould and Fernandez, 1989).

Representatives (**B**) broker in the same way as gatekeepers, however the flow direction of what is being brokered is different, allowing B to represent their subgroup with another subgroup (Fernandez and Gould, 1994, Gould and Fernandez, 1989).

Consultants (**B**) brokers between two unconnected individuals (A & C) both belonging to the same subgroup as each other, but a different subgroup to the consultant (Fernandez and Gould, 1994, Gould and Fernandez, 1989).

Liaisons (**B**) brokers between two individuals in two different subgroups (A & C) to which B does not belong (Fernandez and Gould, 1994, Gould and Fernandez, 1989).

Figure 18. Outlines descriptions for five brokerage roles (Gould and Fernandez, 1989)

8.2.4. Data analysis

Matrices of directed data for the agonistic networks for PC1 and PC2 were constructed in Excel and imported into Ucinet 6, version 6.634 (Borgatti et al., 2002). Sociograms were created in NetDraw (Borgatti et al., 2002). Brokerage typologies and *k*-cores were analysed in Ucinet (Borgatti et al., 2002). Statistical analysis was performed in R.3.4.1 (R Development Core Team, 2017). Data was subsequently tested for normality via histograms and the Shapiro Wilks test. The

data were found to be nonnormally distributed. GLMMs were performed in R.3.4.1 (R Development Core Team, 2017) using the R package lme4, version 1.1-21 (Bates et al., 2015). Upon testing, the negative binomial model was found to be the best fit for the probability distribution. For each model, the pig identification number represented the random effects, and fixed effects (predictor) represented brokerage role (including coordinator, gatekeeper, representative, consultant, and liaison).

8.3. Results

8.3.1 Quantifying missing data

Due to the dynamic nature of the herd, all sows were not consistently present, a result of remixing new sows or removing current sows for farrowing. The data had to be weighted to account for the hours that individuals were absent from the study. In PC1, 15% of the herd (n=12) were missing from the network for 6 hours. In PC2, 15% of the herd (n=12) were absent from the network for 6 hours, and 5% (n=4) were absent for 3 hours. The coefficient, y = n/x, was applied to the degree centrality for missing pigs.

Where:

y = Weighted value of interactions per hour observed

n = Value of either degree centrality or betweenness centrality

x = Number of hours observed

8.3.2. Brokerage role properties: A census at network level

Brokerage roles are not mutually exclusive, and every sow has the potential to assume only one role or multiple roles independently at different times. To account for this variability and construct a network level structure, a census of each sow was undertaken to calculate the frequency to which they engaged in any of the five brokerage roles, coordinators, gatekeepers, representatives, consultants, and liaisons. Analysis of both the aggression networks found that all individuals who lie on the directed path between two others have the potential to engage in brokering aggression within the network. In PC1, 94% of sows and in PC2, 81% of sows participated in some form of brokerage role that allowed aggression to flow through the networks, within and between subgroups. Table 24 outlines the proportionate distribution of the brokerage roles identified within each subgroup in PC1 and PC2.

Table 24. The census count and proportion of brokerage roles within the subgroups in PC1 (n=78) and PC2 (n=78) based upon a census of the frequency that individual sows engaged in each brokerage role including, coordinator, gatekeeper, representative, consultant, or liaison.

Cycle & subgroup	Census of brokerage role (The count)	Coordinator %	Gatekeeper %	Representative %	Consultant %	Liaison %
PC1						
K2	1	0	0	0	100	0
K4	4	0	0	0	25	75
K5	6	0	0	0	33	67
K6	41	2	10	5	46	37
K7	20	0	0	0	75	25
K8	153	1	11	17	41	30
K9	146	1	16	12	48	23
K10	3594	62	13	19	1	3
PC2						
K1	0	0	0	0	0	0
K2	4	0	50	25	25	0
K3	11	5	30	10	35	20
K4	15	0	7	13	40	40
K5	46	0	2	9	65	24
K6	1055	62	14	20	1	3

In both networks, sows in the most connected subgroups (K6 and K10) dominated the coordinator's role, this shows that sows in *k*-core 10 (PC1) and *k*-core 6 (PC2) are more aggressive with each other than individuals in different subgroups, as coordinators only broker between unconnected individuals within the same subgroup. Aggression would become quickly and easily transferred between individuals within these *k*-cores. At a network-level, the role of coordinator proves to be typically occupied by the most connected animals. By comparison, sows in *k*-core 9 (PC1) and *k*-core 5 (PC2), who are still highly connected by the standards of the subsequent networks, hardly engage in coordinating aggression within their subgroup. Instead, these

subgroups are predominantly engaging in consulting (PC1: 48%, PC2: 65%), showing these animals allow aggression to flow between their subgroup and another. They are in effect, receiving aggression from a conspecific in an external subgroup and redirecting the behaviour back into their subgroup to a different individual, thereby allowing aggression to move more freely between their subgroup and a different *k*-core. Sows in the subgroups that are less connected demonstrate substantial variability of behaviour, beyond engaging in coordination. These individuals predominantly engage in consulting but also appear to be flexible to liaising, representing and gatekeeping. Overall, it seems that coordinating, and consulting behaviours are the main types of brokering involved in the transfer of aggression due to similar patterns of structure in both production cycles (Figures 19a, 19b).

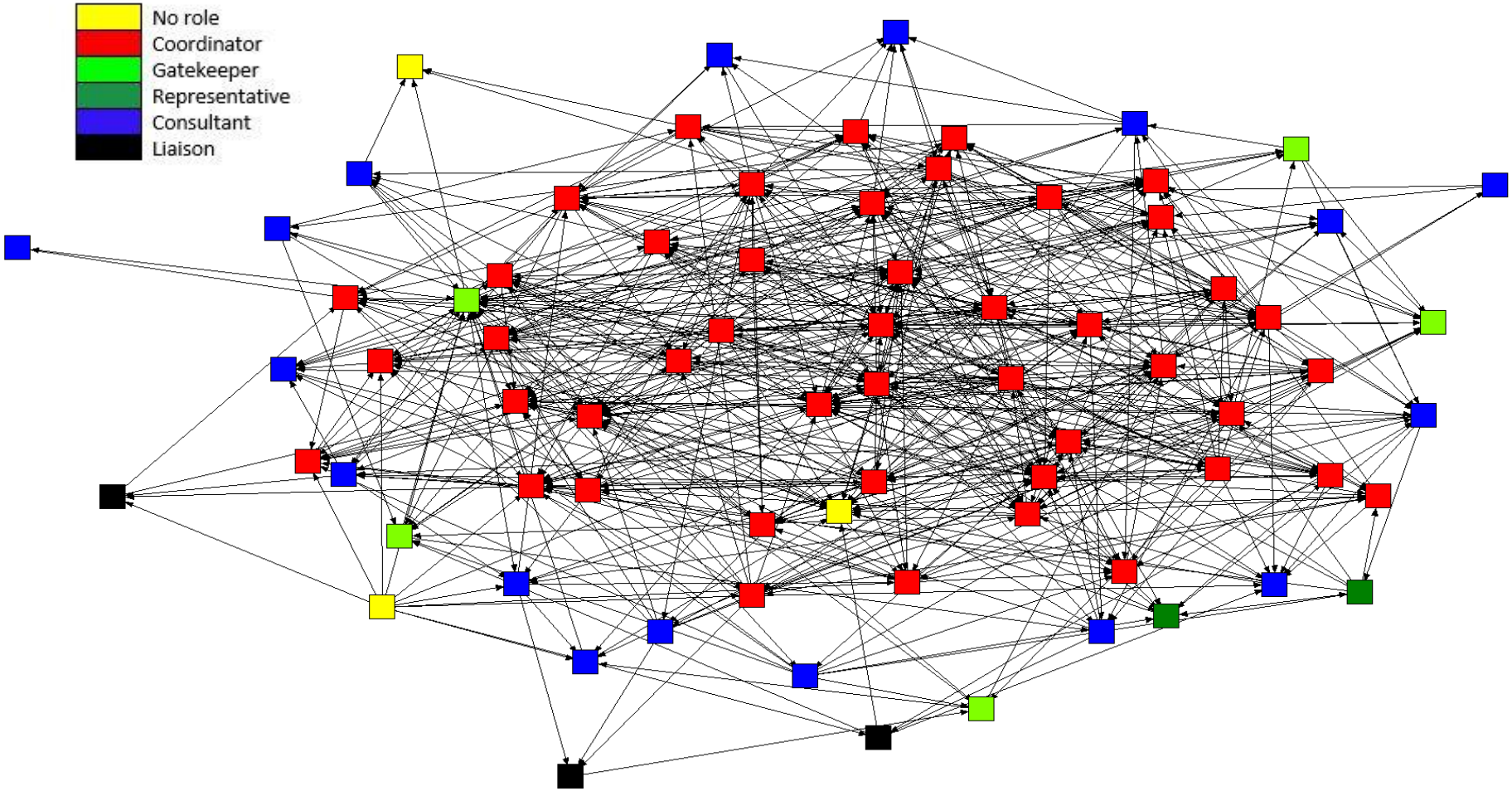


Figure 19a. Directed sociogram showing the agonistic interactions in production cycle 1 (n=78). Arrowheads indicate the direction of interaction and display the initiator and receiver of an aggressive interaction. The legend denotes colour code for brokerage typologies, coordinators, gatekeepers, representatives, consultants liaisons and no brokerage role. Individuals have been assigned to the brokerage role most significant to them using normalised relative brokerage.

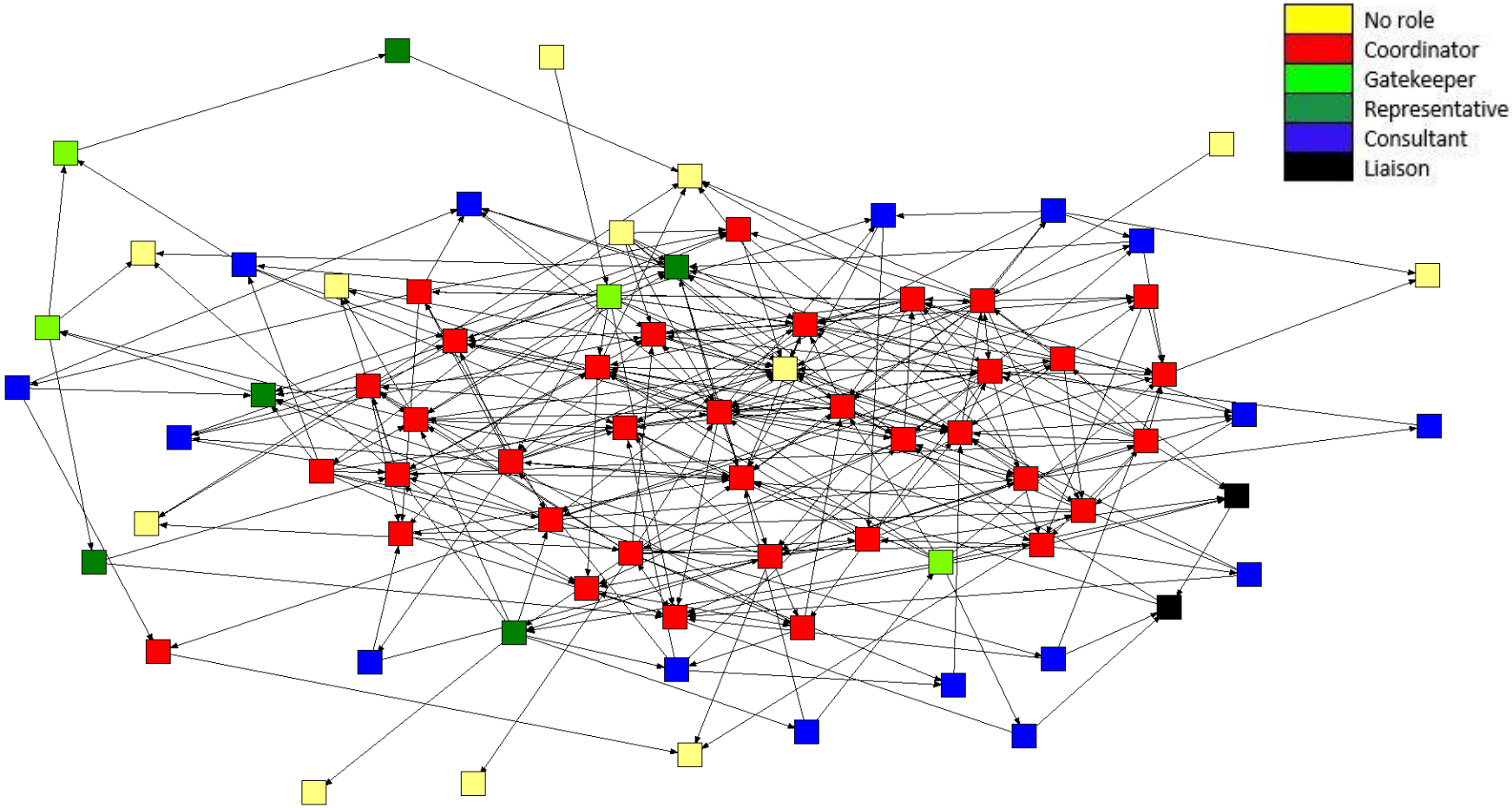


Figure 19b. Directed sociogram showing the agonistic interactions in production cycle 2 (n=78). Arrowheads indicate the direction of the interaction and display the initiator and receiver of an aggressive interaction. The legend denotes colour code for brokerage typologies, coordinators, gatekeepers, representatives, consultants, liaisons and no brokerage role. Individuals have been assigned to the brokerage role most significant to them using normalised relative brokerage.

8.3.3. Brokerage typology and initiated aggression

Aggressiveness significantly affects the brokerage role individuals predominantly engage in both networks. In PC1, sows that predominantly held the typology of coordinator (B1) were significantly more aggressive than sows with no social role (B0) (coef. 2.21, z 4.906, $p < 0.001$). By contrast, in PC2, coordinators, gatekeepers, representatives and consultants were all significantly more aggressive than sows with no brokerage role (coef. 1.42, z 2.47, $p < 0.05$).

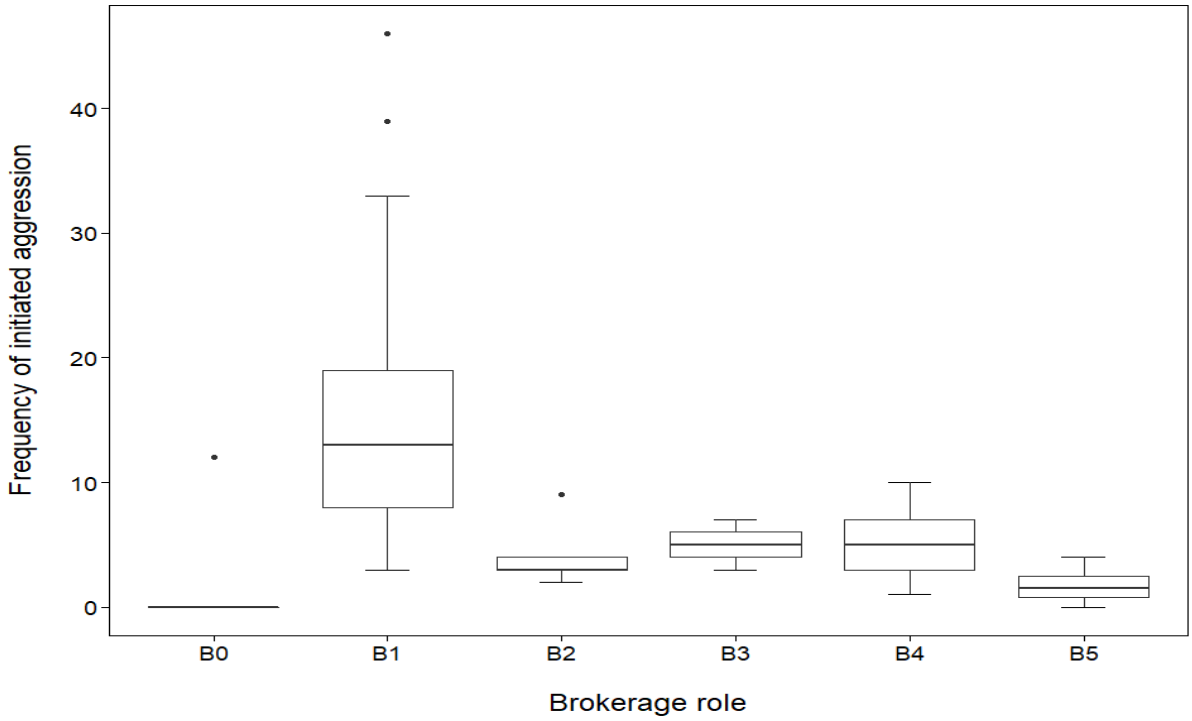


Figure 20a. The frequency of initiated aggression for brokerage roles in production cycle 1 (n=78). Coordinators (B1) were significantly more aggressive than sows in the other brokerage roles with gatekeepers (B2), representatives (B3), consultants (B4) and liaisons (B5) initiating significantly less aggression. Sows with no social role (B0) initiated the lowest rates of aggression (mean 2.4 ± 5.37SD).

In PC1 (Figure 20a), gatekeepers (B2), consultants (B4) and liaisons (B5) initiated significantly less aggression than coordinators (coef. -1.13, z -5.54, $p < 0.001$). Results from PC1 show that the mean frequency of initiated aggression by coordinators was 16.13 ± 10.36SD, compared to the other brokerage roles of gatekeeper (4.2 ± 2.77SD), representative (5.0 ± 2.83SD), consultant (5.0

± 2.78SD) and liaison (1.75 ± 1.71SD). Sows that held no social role were the least aggressive with a mean-initiated aggression value of 2.4 ± 5.37SD.

By comparison, in PC2 (Figure 20b), although coordinators continued to initiate the highest levels of aggression (8.14 ± 8.18SD), they were less aggressive than in PC1. As in PC1, representatives (2.8 ± 2.49SD), consultants (2.88 ± 1.09SD and liaisons (1.5 ± 0.71SD) initiated significantly fewer agonistic behaviours than coordinators (coef. -0.9, z -3.302, $p < 0.001$), however, there was no significant difference between gatekeepers (6.75 ± 5.91SD) and coordinators as was shown in PC1. Overall, the structure of initiated aggression based upon brokerage typology is similar in both networks, despite variations in levels of aggression.

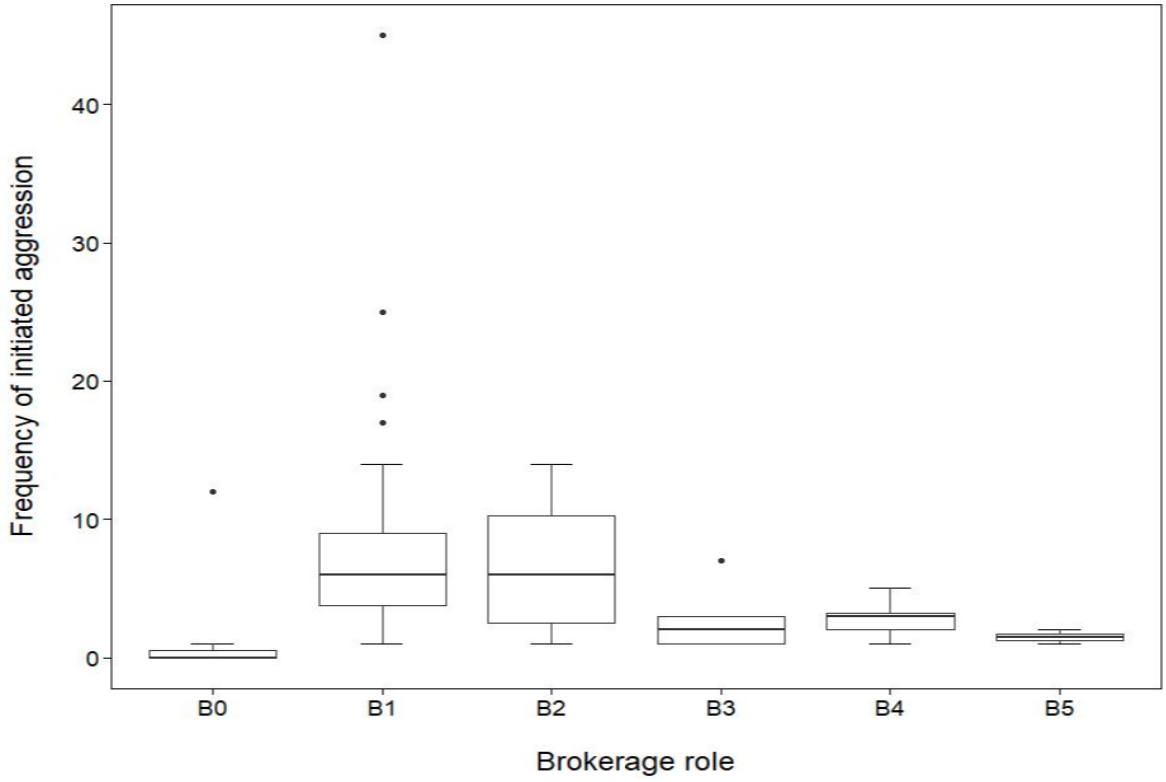


Figure 20b. The frequency of initiated aggression for brokerage roles in production cycle 2 (n=78). Coordinators (B1) were more aggressive than other brokerage roles with representatives (B3), consultants (B4) and liaisons (B5) initiating significantly less aggression. Sows with no social role (B0) initiated the lowest rates of aggression (mean 1.5 ± 0.71SD). B2 = gatekeepers.

8.3.4. Brokerage typology and received aggression

There is a relationship between brokerage roles and the levels of aggression received by individuals in both networks. In PC1 (Figure 21a), coordinators (B1) and gatekeepers (B2) received significantly more aggression than sows which held no social role (B0) (coef. 1.42, z 2.716, $p < 0.05$). Consultants (B4) and liaisons (B5) received significantly less aggression than coordinators (B1) (coef. -.89, z -4.323, $p < 0.001$). Coordinators received higher levels of aggression than the other brokerage roles, showing a mean of 14.28 ± 8.70SD. It is in comparison to the other brokerage roles, gatekeeper (10.8 ± 9.93SD), representative (4.5 ± 3.54SD), consultant (5.71 ± 3.16SD) and liaison (3.0 ± 0.82SD) and those with no social role (4.4 ± 9.84SD).

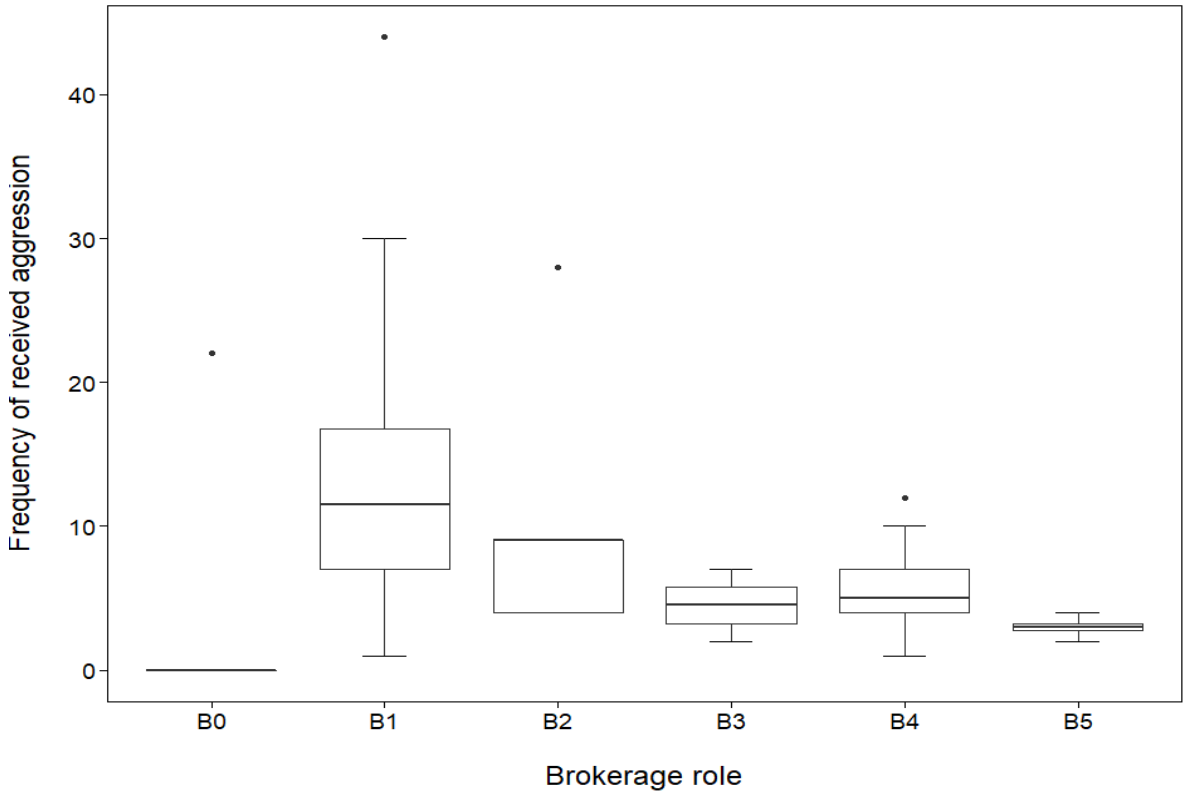


Figure 21a. The frequency of received aggression for brokerage roles in production cycle 1 (n=78). Coordinators (B1) and gatekeepers (B2) received significantly more aggression than sows that held no social role (B0). Consultants (B4) and liaisons (B5) received significantly less aggression than coordinators (B1). Coordinators received higher levels of aggression than the other brokerage roles. B0=no brokerage role. B3=representative.

The pattern of results from PC1 is also reflected in PC2 (Figure 21b); with coordinators (B1) again receiving significantly higher levels of aggression than those with no social role (B0), coef. 1.15, z 4.638, $p < 0.001$. Consultants (B4) continued to receive significantly less aggression than coordinators (B1), as did gatekeepers (B2), coef. -1.04, z -4.493, $p < 0.001$. Overall, coordinators (B1) received higher levels of aggression than other brokerage types with a mean of 7.64 ± 4.42SD. It is in comparison to gatekeepers (1.75 ± 0.96SD), representatives (4.6 ± 4.1SD), consultants (2.69 ± 1.78SD), liaisons (4 ± 1.41SD) and those with no social role (2.73 ± 3.81SD).

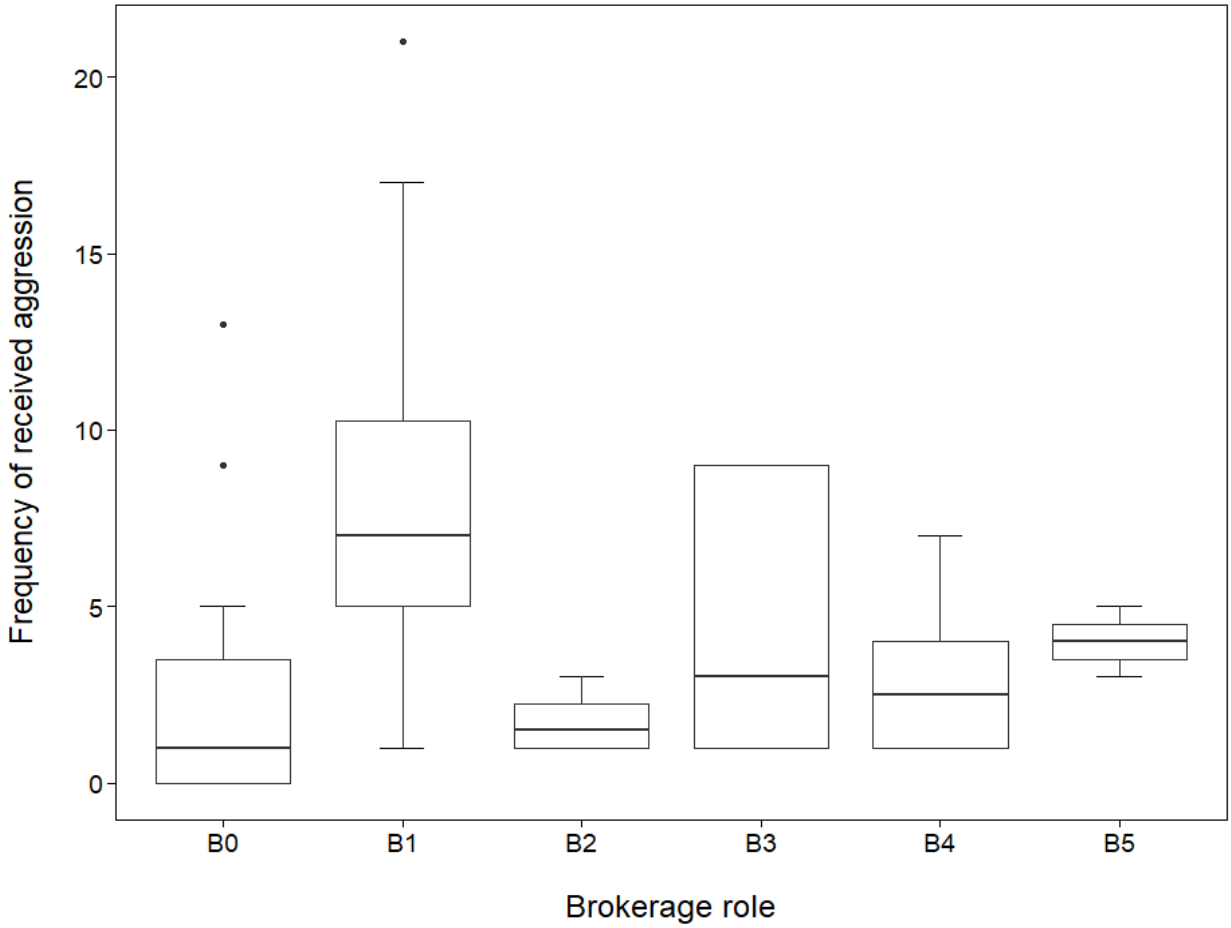


Figure 21b. The frequency of received aggression for brokerage roles in production cycle 2 (n=78). Coordinators (B1) received significantly more aggression than sows that held no social role (B0). Consultants (B4) and gatekeepers (B3) received significantly less aggression than coordinators (B1). Coordinators received higher levels of aggression than the other brokerage roles. B3=gatekeepers.

8.3.5. Consistency of brokerage roles over networks

Results show there is a propensity for sows that predominantly acted as coordinators in PC1 to continue to assume this role in PC2. Of the 35 sows in both networks, 69% (n=24) served as coordinators in PC1 and PC2. Consultants also showed some degree of consistency, with five of the original consultants (n=15) in PC1 continuing to take this role in PC2. No consistency was exhibited in the typologies of gatekeeper, representative or liaison over the two production cycles.

8.4. Discussion

This study found that a significant proportion of pigs have brokerage capacity, with 94% of individuals in PC1 and 81% in PC2 engaging in brokering behaviour. The census further revealed variability in behaviour, with sows capable of engaging in multiple roles, regardless of connectivity based upon the *k*-cores. Gould and Fernandez (1989) presented a methodological opportunity to extend further and characterise a network based upon the five brokerage typologies. These findings show that by continuing beyond the main centrality measures typically associated with identifying keystone individuals, analysis can provide additional information as to how animals are selecting to facilitate information or behavioural flow. Enabling the identification of brokerage types is dependent on the assignment of subgroups. Therefore, subgroups were quantified by how connected an individual was in the aggression networks in both production cycles; a pattern of behaviour based upon connectedness emerges. Regardless of the capacity to engage in multiple roles, sows in the most connected subgroups (K10 & K6) predominantly adopted the coordinator's typology, a position not generally undertaken by individuals with lower coreness values. The most

connected sows facilitated the transfer of aggression not through the entire herd but within their subgroup, acting as internal conduits of behaviour. The most connected sows may potentially adopt these coordinating positions more often due to the size of the subgroups. In both production cycles, the most connected *k*-cores also represented the largest subgroups, highlighting the underlying mechanism of utilising aggression to establish a social hierarchy in a dynamic environment in which centralisation is challenging to achieve and maintain.

Where social stability cannot be achieved, it may be the perception of social rank that motivates behavioural strategy. Within the highest connected subgroups, there is increased competition for dominance, due to the high numbers of individuals, between sows that are seemingly socially equal. The results also show coordinators were the most prolific initiators and receivers of aggression in both production cycles. A lack of facilitation of significant proportions of aggression to external, less connected subgroups, infers individuals in the lower *k*-cores are not considered such a social threat; comparatively, little energy is directed into interacting with them. This pattern of coordinating behaviour is observed in other species exposed to unstable social environments. Hobson and DeDeo (2015) discovered that in newly formed groups of captive monk parakeet (*Myiopsitta monachus*), individuals developed a strategy in which aggression was directed more frequently towards those considered close in social rank. A network study of pukeko (*Porphyrio melanotus melanotus*) also suggests an increased likelihood of fights between birds close in dominance rank (Dey and Quinn, 2014). By comparison, this behavioural strategy was not demonstrated in any of the other subgroups in both production cycles, despite modulations in brokering taking place.

Sows within the mid-range connected subgroups, in PC1 (K9, K8, K7 & K6) and PC2 (K5, K4, K3), did not generally engage in coordinating behaviour. Although there was variability in brokering behaviour at an individual level, sows in these *k*-cores predominantly adopted consulting. Consultants broker between two unconnected individuals belonging to the same subgroup, but a different subgroup than the consultant. These sows are in effect, redirecting aggression away from their subgroup and keeping it internalised in another. Compared to the highest connected subgroups, these *k*-cores held significantly fewer but similar numbers of animals. The differences between the most connected subgroups and the mid-range subgroups again indicate variability in behavioural strategy and aggressiveness. Overall consultants were found to be significantly less aggressive and received less aggression than coordinators. It also shows that sows within the least connected subgroups in PC1 (K5, K4, K2) and PC2 (K2, K1), overall were more likely to act as gatekeepers or liaisons. Gatekeepers broker between unconnected individuals, one within the same group as the gatekeeper and one in an external group. By comparison, liaisons broker between two unconnected individuals who belong to a different subgroup from each other and the liaison. The nature in which liaisons can transfer behaviour over a wider range of conspecifics suggests they could be viewed as potentially the most efficient brokers. Very few examples, however, of liaising behaviour were observed. Gatekeepers are the only brokers who can enable the transfer of a behaviour from an external subgroup back into their own. Previous work on brokerage typologies has been outside the realm of animal science and predominantly focussed on the role of gatekeepers in information flow networks (Boari and Riboldazzi, 2014). Correspondingly, to numbers of liaisons, there were also very few examples of gatekeeping behaviour observed. Describing the configuration of brokerage roles in a network enables a

clearer picture of the flow and transference of a process (Kirkels et al., 2010). The absence of a brokerage type, such as gatekeepers and liaisons, maybe just as informative as identifying the presence of a brokerage type. Accordingly, certain brokerage types play different roles within specific transfer networks.

Adoption of specific brokerage types within the subgroups over the two production cycles indicates inference of social information (Hobson, 2020) that must be beneficial in some way to the individual. The lack of coordinating behaviours in the mid and low subgroups reflects more robust social stability than in the highest connected subgroups, a pattern of behaviour observed in smaller wild boar herds (D'Eath and Turner, 2009). The individuals within the mid and low subgroups are not transferring aggression through their *k*-core. They are instead acting as external conduits of the behaviour. While there may be perceived benefit to attacking subgroup conspecifics in K10 and K6, there does not appear to be any benefit to this course of action in the other subgroups. Boumans et al., 2018, suggest that beyond a point of competition, it is a behavioural strategy that determines the frequency and type of interaction. The stability of the findings over two production cycles demonstrates behavioural strategies are being employed at the group level that influences the manner which aggression is being transferred through the herd via the types of brokerage typologies observed.

There are two possible explanations for the differences in brokerage preferences observed between the *k*-cores. Firstly, subgroup size may be the key to the stability and behavioural strategy that, in turn, determines the type of broker, and aggressiveness that could be expected. A

hypothesis supported by recent research (Johnson-Ulrich and Holekamp, 2020) into the effects of clan size on expected rank behaviour in wild spotted hyaenas (*Crocuta crocuta*). In commercial animals, particularly poultry and pigs, group size is a foremost determinant of increased aggression (Rodenburg and Koene, 2007). Past a point of undetermined subgroup size, aggressiveness will mainly become directed towards subgroup conspecifics, as represented by coordinating behaviour. The limitations of potential fighting opponents within the smaller subgroups must be considered as the group size may indicate an increased likelihood of fighting with an individual from another subgroup. Likewise, it may also be more likely that within larger subgroups, where fighting opponents are more readily available, the chances of internalising aggression within that subgroup would increase. Secondly, subgroups usually consist of individuals with common goals or similar traits (Borgatti et al., 2018). In this instance the similar characteristic is connectedness and, the common goal appears to be firstly maintaining a more connected position in the aggression networks for those in K10 & K6, a hypothesis supported by the stability of adopting the coordinators' role over two production cycles. Furthermore, brokerage typology may be a strategy for advancing social position by acting as an external conduit of behaviour towards other subgroup conspecifics. Expressing a desire to engage more aggressively with external subgroup conspecifics through brokerage roles, that ultimately impact upon social position, is also consistent with the behavioural instability that has been evidenced in the previous chapters.

8.5. Conclusions

This preliminary investigation into the application of brokerage types to describe network structures in an animal social network demonstrates it is a potentially valuable technique to extend upon the traditional centrality metrics currently applied. It is further providing a criterion to describe social roles that extend beyond just identifying brokers through significantly high betweenness centrality. The application of the technique shows that network structure, based upon typologies, remains consistent over time despite sows having the potential to engage in multiple brokerage roles. The highest connected sows consistently engage in coordinating behaviour, fundamentally keeping aggression internalised within their *k*-core. Lower connected sows transfer aggression externally with and through other subgroups. The findings reveal that subgroup size is a determinant for predicting aggressiveness and how behaviour gets transferred through the herd. This study is the first known to investigate this network metric in animal behaviour research; it paves the way for supporting future research by extending subgroups to account for other variables such as parity, size, welfare, or productivity.

Chapter nine

General Discussion

9. General Discussion

9.1. Introduction

The 2013 ban of sow stalls provided a pivotal turning point for the welfare of gestating sows, allowing for freedom of movement and the ability to perform natural behaviours. The new regulation engendered large grouping sizes, placing more unfamiliar animals together in dynamic systems; this has given rise to a new welfare crisis. There has been extensive research into the development of procedures to reduce aggression in group-housed sows, a detrimental behaviour both to the physiological and psychological wellbeing of individuals and to reproductive performance. Despite the abundance of this work, aggression continues to be a considerable economic and welfare concern (Peden et al., 2018). In recent years, research aims have begun to turn towards positive behaviours as a mechanism for improving welfare and reproduction (Rault, 2012). Changing the approach from investigating aggression to positive behaviours can extend our understanding of the complexities of the social relationship benefits of significance, ensuring an enhanced comprehension of herd sociality. Sociality exists in two spectrums, at group level and an individual level; individuals, are separate entities, guided by multiple intrinsic and extrinsic variables.

How gregarious individuals respond to the social environment and their conspecifics can impart effects, both positively and negatively, throughout a social group. Only by peeling back the layers of sociality can animal scientists gain further insight into these complexities. Social network analysis has become a valuable tool, transitioning observations, and enabling investigations at a

micro-level; a must-have precondition to answer the entanglement and effects of sow behaviour. There are successful documented applications of SNA in the fields of ecology and conservation (e.g., Robinson et al., 2018), revealing it as a valid measure that can be applied at multiple levels of social complexity, capable of enhancing research in the field of animal science. The aim of this thesis was, therefore, to apply social network metrics to investigate the social structure of a dynamic herd of group-housed, gestating sows. The primary objectives were to evaluate the herds' social structure and identify key animals, then further investigate the temporal nature of these social roles in an unpredictable and challenging social environment. There is a continued need to seek out novel management strategies to reduce aggression.

The thesis begins with a general overview of social structure in the context of preferential associations, attempting to answer the outstanding question of, “do pigs have friends?” Chapters four and six identify social roles through the creation of preferential association and agonistic networks, further evaluating the stability of prominence and influence over three production cycles. In chapters five and seven, the impact of social roles on reproductive performance is evaluated. Finally, chapter eight extended beyond the traditionally used social network metrics, applying brokerage typologies. The findings of this thesis are summarised in the following paragraphs, assessing the limitations of the work, putting the research into the context of practical application, and identifying future directions.

9.2. The social structure of a dynamic sow herd

The primary objective of Chapter three was to describe the social structure of the herd in the context of preferential associations, allowing for new insights of sociality beyond the traditional evaluations of aggression. Behavioural observations occurred during only one production cycle to provide a snapshot of social structure. Social bonds are established in other commercial species (i.e., Boyland et al., 2016); the value of positive relationships in welfare terms is essential, with advantages for wellbeing, health, and reproductive performance (Silk et al., 2009; Rault, 2012). The results revealed low rates of preferential associations at every network threshold, with only five interactions shown as the maximum number of positive ties between any initiator and the same recipient. It was necessary to apply network filters to distinguish between random and non-random interactions. Visualisations of the original, mean and 1.5 x mean networks showed the cohesiveness of the networks substantially declined as the threshold filter of interactions to be included in each network increased. The 1.5 x mean network, in which the threshold of interaction was set at ≥ 3, only contained 42 animals of the original network, revealing nine components (six of which were dyads) and only two reciprocated interactions. The lack of cohesiveness was supported by low-density levels in every network, indicating that individuals did not engage in many of the potential interaction opportunities available, despite unrestricted access to functional areas and conspecifics. A lack of propensity to establish more sustained preferential associations as the threshold level increased are supported by the mean degree in each network. Scarcity of positive ties was additionally revealed with a low rate of interaction in positive nasal-nasal contacts.

The findings are consistent with previous research, that also document affiliative behaviours as being rarer in commercial herds than agonistic behaviours (Foris et al., 2018). The question arises

as to why; strong bonds are beneficial to fitness and survival, so it might be expected that in a dynamic herd, sows would seek to establish strong bonds to mitigate a challenging environment. However, the social context may have a more profound effect on the construction of ties and the extent to which their strength is of value. In Barbary macaques, *Macaca Sylvanus*, and vervet monkeys, *Chlorocebus pygerythrus*, there is a positive correlation between positive bonds with conspecifics and survival, due to extreme weather conditions during winter months (McFarland and Majolo, 2013; McFarland et al., 2015). In these examples, it is the number of bonds, not the quality, that is of value, and this is an important distinction and one that must be applied to the current findings. Not all species engage in strong affiliative relationships to access fitness-enhancing benefits. For example, the low quantity of socio-positive behaviours in the sow herd is in line with recent research into the quality of social bonds. Silk et al. (2018) studied a wild group of female chacma baboons, revealing that although individuals did form some strong ties, it was the development of weak ties that enhanced reproductive success. Weak ties develop if there is little or no reciprocation in behaviour. The benefits of bonds, therefore, are a significant motivator for their level of development and sustainability. Reflecting a behavioural mechanism in the Sturgeon's farm sows that is potentially accessing some form of social support, adapted, and derived from the social context, and physical environment. However, it must be acknowledged that despite mechanisms introduced to discount random interactions in the herd, such as the threshold levels, the caveat of non-social lying choices remains. This is In line with other related literature (Durrell et al., 2005; Goumon et al., 2020) which reports the same caveat. Despite the finding that lying preferences are seemingly motivated by a recipient's connectedness, there is also the consideration that subordinate sows may select resting partners due to restricted lying

area access. For example, subordinates may return to rest with the same individual multiple times if they are simply tolerated, rather than a social discriminatory choice motivated by the personality or other traits of the selected resting partner.

This behavioural strategy is revealed when extending beyond the descriptive statistics. At first glance, the metrics indicate that commercial sows are not forming sustained social bonds, a finding in conjunction with previous research (i.e., Durrell et al., 2004). The application of SNA, in this study, allowed for the transition from group-level to individual-level behaviours, a method not employed previously. At this level of analysis, it becomes clear that the picture of behaviour is intrinsically complicated. In all three networks, centralisation was low, indicating a level of social equality between conspecifics. When *k*-cores were applied to the mean network it was revealed that four subgroups were present, although sows were not connecting at a high rate, individuals within the largest *k*-core (K4) were more socially central within the network. The advanced analysis of the *k*-cores further revealed that sows in K4 were not just more social, initiating significantly higher rates of approaches than conspecifics, but were also more popular by receiving considerably higher levels of approaches, indicating that the pigs are not socially equal. While the findings do not show the development of mutual friendships, they reveal that preferential associations are occurring and crucially that positive associations do not have to be bidirectional. There are individuals within the dynamic herd that are preferable for interaction, regardless of a lack in reciprocation of behaviour, indicating a quality of bond not previously considered. It is a finding supported by a recent SNA study of grooming behaviour in dairy cattle, in which asymmetric ties were substantially more frequent than mutual ties (Foris et al., 2019). Lack of

reciprocation in the current study influenced the strength of the bonds, ensuring that friends of friends will not become friends in this unstable environment, further reflected by the low clustering coefficients in each network.

There was no positive assortment by parity or familiarity, supporting previous research of commercial pigs (Durrell et al., 2004), despite similar traits identified as motivators to form preferential ties in other commercial animals (Boyland et al., 2016). In the absence of homophily by trait, it suggests in the preferential association mean network, individuals in this study were socially discriminating for another reason. Potentially discrimination occurred due to the perceived sociality of a conspecific by a behavioural initiator. The results show that increased sociality raises an individual's social 'profile', making them more desirable for interaction. The finding is in line with the recently proposed concept of 'valuable social partners' (Kulahci and Quinn, 2019). It remains unclear though what the benefits of associating with a highly connected sow may be. Valuable social partners provide a fitness-enhancing trait that benefits conspecifics, in the absence of available benefits, such as access to important foraging sites, the most likely motivation at Sturgeons farm would be preferred resting space. In this instance, an individual would not require reciprocation of behaviour, just merely social indifference, a response also demonstrated in poultry (i.e., Abeyesinghe et al., 2013). At a group level, the results show how individual variance in sociality has the potential to affect social structure and cohesiveness. Indicating that despite low centralisation, there are individuals within the herd with the capacity to disproportionately affect the group, advocating additional support towards investigating and identifying key animals (chapters four and six).

9.3. Identifying socially prominent and influential sows

The main objective of Chapters Four and Six required the identification of key animals based upon their disproportionate prominence and influence within the herd. Behavioural observations of agonistic behaviours and preferential associations were collated to analyse the stability of behaviour, investigate individual variations and social role. The application of *k*-cores to the behavioural networks over three production cycles revealed subgroups in every network, reflecting inequality of sociality. Socially prominent and influential sows presented throughout the herd in all networks. Interestingly, the numbers of SPS and SIS generally remained consistent over the production cycles between each behavioural network. Despite the networks consisting of variable compositions of sow numbers, individual sociality, and substantially more aggression than preferential associations, results indicate an element of structural stability at the group level. In wild boar and stable social groups, hierarchies are linear with evident centralisation (Gonyou, 2001), so it might have been expected that only sows in the most connected subgroups would identify as either SPS or SIS. However, the results revealed connectedness was not predictive of the power and influence at an individual level as all sows, regardless of *k*-value, could be quantified as either SPS or SIS. It is a significant finding, demonstrating there is the development of micro-hierarchies based upon connectedness (supported by the E-I index findings in chapter three) within the herd, independent of the whole group structure. SPS or SIS in a low connected subgroup can exert the same effect on subgroup conspecifics as SPS or SIS quantified in a highly connected subgroup. The main findings demonstrate that sociality or the perception of rank is not a prerequisite for becoming socially prominent or influential in this dynamic herd. This result conflicts with previous research of wild animals (i.e., Andersen, 2005a) but supports recent

research of commercial dairy cattle (Machado et al., 2020). Regardless of connectivity, SPS and SIS are disproportionately more powerful or influential than subgroup conspecifics. Secondly, if keystone individuals are distributed throughout the herd, even on the social periphery (as would be the case with an SPS or SIS quantified in a K1 or K2 subgroup), it will have implications for how disease outbreaks or intervention strategies are managed (i.e., Change and Sih, 2013; Robinson et al., 2018). Also, it will inform predictions of potential outbreak risks if there are substantial numbers of SIS within a network. The study extends understanding of which animals may impart positive or negative effects on a social group, providing a new perspective. Finally, the findings continue to provide support for social network analysis as a valuable tool concerning the welfare of commercial species; demonstrating that key individuals can be identified even in intense and dynamic commercial systems.

9.4. Social prominence and influence in the preferential association networks

The results contained in Chapter four uncovered being either socially prominent or influential in the preferential association networks was not generally a stable trait observed throughout the production cycles. Only 35% of SPS and 10% of SIS were quantified more than once and, there were significant differences in individual behaviour between production cycles. The differences indicate behavioural flexibility that is socially-context dependant, a finding consistent with the research of dairy cattle. Foris et al. (2019) found that cows altered their behaviour in response to which individuals were in a network at any given time. Although the current study did not support bidirectional preferential ties, it does reveal there is social discrimination in favour of more highly connected sows. The instability of social prominence and influence in the preferential association

networks support the findings of chapter three. If a favoured conspecific gets removed from the herd, an individual may not just necessarily replace them with a less favoured sow. Almost certainly it will have implications for welfare; positive interactions enhance wellbeing and reproductive performance, whereas restricted access to a preferred resting partner could impair overall health and reduce social support. In this social herd, one of the main findings of chapter four reveals degree centrality and betweenness centrality are not stable social metrics, unable to be utilised as predictors of individual behaviour in the preferential association networks.

Chapter five aimed to investigate the relationship between social prominence and influence in the preferential association networks and reproductive performance. Recent research has begun to evaluate the impact of positive behaviours on reproduction and offspring survival (i.e., Silk et al., 2009; Schülke et al., 2010), highlighting this avenue of research as a potential mechanism for improving reproduction in commercial sows. The principle finding revealed that stillbirth numbers appear to be the only production metric significantly impacted upon by social role. SPS consistently demonstrated lower rates of stillborn piglets than non-SPS over three production cycles. Overall, although a weak negative correlation was found between degree centrality and numbers of stillborn piglets, when the sows were classified as those with stillbirths and those without; sows with stillbirths demonstrated significantly lower degree centrality than those without stillborn piglets. However, there was a lack of effect on the numerous other reproductive metrics. No relationships were found between SPS and non-SPS, and the reproductive traits including, mummification, low viability, crushing, hypothermia, starvation, lameness, and scours,

despite SPS presenting with a lower mean prenatal mortality rate than non-SPS in all three production cycles.

Social influence did not impart the same level of impact on reproduction, with SIS displaying fewer stillbirths than non-SIS in only two production cycles and again no relationship between social position and any other reproductive metric. Despite a significant moderate, negative association between betweenness centrality and stillborn piglets, at the network level, social influence did not appear to impart the same effects as social prominence. These differences are potentially due to the mechanism in which behaviour is transferred, degree centrality reflects the positive or negative consequences of dyadic interactions, unlike betweenness centrality, that affords greater reach through a network. Sows may benefit from dyadic preferential interactions, even if unreciprocated; however, there may be less motivation to 'pass on' this type of behaviour. Preferential interactions can be defined as many behaviours in multiple species including, sniffing, licking, proximity, and allogrooming. While proximity and any positive behaviour are necessary for a behaviour to be transferred, in this study, a preferential association was defined as tolerated proximity during resting. Therefore, 'passing-on' the behaviour could only be achieved if the recipient displaced herself and then moved to a preferred conspecific. Furthermore, as there was little clustering occurring, an indication of low triadic closure, it would be unlikely that transference would freely be observed in the herd. Overall, the chapter indicates that direct interactions seem more impactful on stillbirth numbers than indirect interactions, with degree centrality, rather than betweenness centrality, a more meaningful social network metric to apply to future related work. However, future work is required to directly isolate the actual cause of

stillbirths to disentangle social influences and biological processes including farrowing duration, infectious and non-infectious causes.

9.5. Social prominence and influence in the aggression networks

Chapter six revealed that as with the preferential association networks, social prominence in the aggression networks was also found to be an unstable individual behaviour. Only 28% of SPS quantified more than once and with significant changes in initiated aggression between production cycles. Plasticity in aggression indicates that sows are possibly altering behaviour in response to changing conspecifics, demonstrating individual-level decision making. Engagement in aggressive encounters can be costly (Estevez et al., 2002), and the sows at Sturgeons farm are revealing they have the capacity to 'size-up' potential opponents or be remembering previous encounters and react accordingly. The findings are consistent with previous research in which behavioural response is context-specific (i.e., Krause et al., 2010; Foris et al., 2018). The overall levels of agonistic interactions remained high during all three production cycles, maintaining similar social structures. Levels of aggression may have been contributed to via the feeding pattern implemented by the electronic sow feeders, which were reset daily at 15:00 h. Sows exhibit a diurnal pattern of feeding behaviour and will have a strong motivation to feed in the morning; 73% of feeding activity in group-housed sows is shown to be between 06:00 h and 18:00 h (Dourmad, 1993). When diurnal patterns of feeding are disrupted, levels of aggression will increase along with reduced welfare and reproduction (Vargovic et al., 2021).

There were similar numbers of SPS and SIS in each production cycle and quantified sows distributed throughout the herd, yet the structure at an individual level was less predictable. This result is an interesting development, as it might have been expected that at a network level, the overall social structure would be less stable. However, recent work in the application of social balance theory to primate groups could shed light on the results. Social balance theory employs social network analysis to evaluate social stability through the investigation of dyadic and triadic patterns (Wasserman and Faust, 1994). Gelardi et al. (2020) conducted a three-year study to investigate the stability of a wild group of Guinea baboons, *Papio papio*, based upon signed triadic relationships. As with the current study, Geraldi et al. (2020) found that at first glance the overall network structure appeared stable, however, at an individual- level baboons were altering their behaviour in the types of relationships they engaged in and with whom they interacted. Although this thesis found little evidence of triadic closure in the preferential networks, this recent development encourages future work which details social balance through the application of signed interactions for further analysis of individual behavioural changes to be performed.

Compared to social prominence, transitivity of social influence in the aggression networks revealed a more complex picture of behaviour. At the network level, only 20% of SIS quantified more than once, at an individual level betweenness centrality was more stable, with no significant differences in the social metric in any of the production cycles. Identifying betweenness centrality as a stable metric is valuable for informing strategies on the potential rate and speed of any behavioural or disease transmission in a group. Furthermore, since SIS are identified throughout the aggression networks, in both the low and highly connected subgroups, this demonstrates that

the potential 'reach' of negative behaviours or diseases in this herd is high, particularly if sows are assorting by connectedness. This work is supported by a recent study which also promoted betweenness centrality as a valuable tool in the prediction of aggression in pigs (Foister et al., 2018). The findings provide an alternative perspective of which animals may impart the maximum effect at a group level, with betweenness centrality identified as a predictive measure of individual influence in the aggression networks.

While there is extensive evidence of the impact of received aggression on reproduction and maternal behaviour (i.e., Cronin et al., 1996; Rutherford et al., 2014), insufficient knowledge of the effects on the individual that initiates the aggression is known. It might be expected that disproportionately aggressive individuals in despotic societies would have improved reproductive performance, an indirect effect of improved access to valuable resources or mates (King et al., 2011; Surbeck et al., 2012). However, the findings of chapter seven reveal conflicting results; in the analysis of one farrowing event after each production cycle, there were no consistent differences in any of the production metrics between SPS and non-SPS or between SIS or non-SIS. This inconsistency was also reflected in a lack of correlation between outdegree centrality, betweenness centrality and the production metrics. When accounting for two farrowing events, both non-SPS and non-SIS had increased stillborn piglets in the second farrowing. However, a lack of social information prior to the second farrowing cannot confirm a relationship between the reproductive metrics and social position over time despite previous research indicating that it is chronic aggression that impedes reproduction (Turner et al., 2005). The study shows that a

longitudinal approach, investigating social position and production metrics over multiple farrowing events, is required for future work.

9.6. The application of brokerage typologies

The application of brokerage typologies, has to the researcher's understanding, never previously been applied to social network studies in animal science. It extends beyond betweenness centrality by identifying the specific nature of brokering activity at an individual level (Chauduary and Warner, 2015). While individuals can engage in multiple brokering roles including, coordinator, representative, gatekeeper, liaison and consultant, there is the potential in specific roles to be disproportionately engaged. Chapter eight investigated brokerage typologies by connectedness (*k*-core) in the aggression networks over two production cycles. The findings of this chapter revealed gestating sows are strikingly capable of engaging in brokering behaviour and that connectedness determines one's adoption of a specific brokering manner. In both production cycles, sows in the highest connected and largest subgroups predominantly undertook coordinating roles, meaning a substantial proportion of behavioural transmission was occurring within a subgroup and not between subgroups. The findings are consistent with recent studies of birds, where there was a higher likelihood for aggression to occur between individuals of similar social standing (Dey and Quinn, 2014; Hobson and DeDeo, 2015). In contrast, the lack of coordinating behaviour in the lower and smaller *k*-cores indicates that these individuals are transferring aggression between subgroups rather than within them. The chapter reveals further, valuable insight into the complex structure of a dynamic sow herd and the impact of subgroup size, that despite the development of subgroups there may be a threshold at which stability

cannot be maintained. Until now, brokerage typologies in gregarious species have merely been inferred (i.e., Farine et al., 2015). This work provides support for the application of brokerage typologies to other species, both wild and domestic. Ensuring meaningful, clear criteria and a definition of brokerage activity; a new methodology to investigate the relationship between brokering behaviour and a multitude of variables that may impact welfare, conservation, or reproduction.

9.7. Limitations of the work

The thesis was limited to the observation of one study herd, within a specific production system, although the research consisted of datasets for different behaviours (as in Foris et al., 2019) over three production cycles. The observation of one study herd of pigs in a specific production system over multiple remixing events is consistent with similar studies (Büttner et al., 2015a; Büttner et al., 2015b). Although the herd's dynamic nature provides limitations to the application of the findings to other housing systems, as behaviours in stable systems may be less variable than in a dynamic system, many of the findings are consistent with current and previous related research. Continuing to shed new light on the complex behaviours of commercial species and supporting positive behaviours as welfare markers of wellbeing and reproductive success. The principles of social network analysis promote an opportunity to transition one technique to other networks (Castles et al., 2014), supporting the application of the techniques in identifying socially prominent and influential animals to any given system, herd, or social group.

The thesis included degree as a direct measure of centrality and betweenness as an indirect measure of centrality. Although these centrality metrics are in line with related studies, there are multiple measures that are also commonly applied to SNA of animal behaviour including eigenvector centrality, reach centrality, farness centrality, closeness centrality, information centrality and strength of ties (Brent, 2015; Borgatti et al., 2018). The clustering coefficient is also a common measure but was included in chapter 3 to assess the preferential associations found in production cycle 1. Applying multiple metrics is beneficial as it provides a deeper overview of the group structure with each metric relating to a different facet of the social interactions. For example, in the current study sows were categorised by how connected they were with the application of the *k*-cores. The *k*-cores provide some information on the connectedness of an individual that is interacted with but does not provide information on the quantity of ties. Other related work (e.g., Turner et al., 2020) has additionally applied eigenvector centrality, the application of which may have strengthened understanding of the social ties in the current study by providing information on both the quantity of social ties between individuals and how connected they were.

There were also limitations to the study concerning nasal interactions; the original aim was to include preferential associations and positive behaviours in the analysis. However, extremely low levels of positive interactions occurred. There are two likely explanations for the lack of positive behaviour data. Firstly, previous research on nasal contacts has also implemented an all occurrences recording method. Still, unlike the current study, it observed focal animals rather than attempting to look at the whole group (i.e., Camerlink and Turner, 2013). It indicated focal

observations provide a more reliable technique for data collection in a large group (Martin and Bateman, 2007, p. 49). The more likely explanation is, due to the high clarity of video footage, positive behaviours may not have been detected because they simply were not occurring at such a high rate as the agonistic interactions. Although preferential associations were more easily detectable, the threshold of these repeated encounters was low, with only a maximum of five interactions recorded in any network between an initiator and the same recipient. In conjunction with the lack of positive behaviour data, this may support the lack of symmetric social bonding in the herd. A further limitation to the observation of low threshold levels of preferential associations relates to the amount of behaviour data captured. Despite the pilot study identifying the times of the day when the sows were most active, the provision of substrate enrichment has been documented to increase resting and sleeping behaviour later in the day (Nasirahmadi et al., 2017). Prolonged resting periods may have resulted in fewer preferential interactions and an increase in observation periods for these positive behaviours may have been more appropriate.

The final limitation relates to chapters five and seven, which investigated the effect of social role on reproductive performance. The initial analysis looked at the impact of social position at an individual level on reproduction directly after a sow had been removed from the dry barn to the farrowing house. Although there was access to information pertaining to the second farrowing event, the time delay between farrowing meant that even if it could be determined how many times an individual had been quantified as SPS or SIS (during the three months of the study), it could not be determined what social position a sow held directly before the second farrowing event. Despite this, the findings are in line with previous work highlighting the impact of sustained

behaviour on reproduction, for example, sows quantified as SPS more than once did have substantially lower rates of stillborn piglets than their conspecifics.

9.8. Future directions and applications

Social network analysis is proven as a valuable tool for the assessment of sociality and social roles in many species, despite an underrepresentation for commercial animals. This thesis demonstrates that key animals can be identified within intense and dynamic systems, providing a platform for future work in which the impact of individual-level social roles on group level dynamics can be further investigated. The Sturgeons farm study informs future related work by differentiating between the social network metrics, highlighting their value within different behavioural contexts. In 2015, Brent remarked on the need to explore the relationship between animals that are highly connected indirectly and their less indirectly connected conspecifics. This study provides insight into that relationship; betweenness centrality, which was found to be a stable trait in the aggression networks, rather than degree centrality indicates the importance of indirect interactions for the welfare of commercial pigs. The application of which is to provide an alternative yet predictive measure of an individual's impact factor. The social position would also be a useful welfare marker for predicting future reproductive success, as is observed in other species, serving as a mechanism for identifying behavioural or disease transference capacity throughout the herd. There are multiple opportunities to implement the techniques of identifying social prominence or influence into other production systems and herds. A greater understanding of the impact of individual position within a herd could easily be extended to alternate systems

including stable systems, loose-housed sows, and outdoor pigs, variable group sizes and composition.

By extending beyond betweenness centrality to brokerage typologies, the current study indicates a future, novel avenue through which to gain a greater understanding of the dynamics of brokering behaviour within and between subgroups. Social network analysis allows for the identification of subgroups incorporating a multitude of variables that can be assessed, such as, subgrouping by parity, familiarity, size, or breed. Brokerage typologies allow an extension on this insight by determining how the subgroups are composed and how they impact at a network level. An example of one application of brokerage is demonstrated in the new concept of complex contagion. Studies of simple behavioural contagion postulate that it is social centrality that aides the transmission of behaviour or information, so an individual with greater connections would be more influential (i.e., Kulachi and Quinn, 2019). However, a recent review proposed that contagion is not limited to social connections but extends to how individuals receive information or behaviour and how this feedback moves through a group (Firth, 2020). Brokerage typologies do not depend solely on the frequency of social connections but rather the nature of transmission; a network dominated by coordinators indicates contagion would be predominantly confined within subgroups, whereas a network dominated by liaisons suggests an increased probability of contagion throughout the entire social group, due to the manner these brokers transfer behaviour. Therefore, the application of the brokerage concept would be particularly advantageous to the assessment of subgroup formation in new, captive, social groups; a lack of or dominance of a type of brokerage role may provide valuable information as to the flow and

transmission of behaviour or disease through a network (Kirkels and Duysters, 2010). This approach is multi-disciplinary and could be applied to any animal behavioural network in future work.

When considering sociality in terms of reproductive performance, the thesis gives support to implementing strategies based upon positive behaviours. By identifying a relationship between social prominence in the preferential association networks and reduced stillbirths, the study reveals the application of a welfare marker both for the sow and offspring survival. The study also reveals the importance of longitudinal observations in future work, where multiple farrowing events and stability of social position can be assessed. To establish if gestating sows in unstable environments can form long-term, reciprocated social bonds, further analysis of the relationship between preferential associations and positive behaviours is required. This direction of research has implications for wellbeing, as the ability to cope with challenging environments can be alleviated by mechanisms of social support. Finally, In the absence of a relationship between litter size and social role, in the context of piglet deaths at farrowing, an important future direction is to understand further the impact of social role on the neuroendocrine system, indicating a need for a multi-disciplinary approach.

9.9. Conclusions

The overall aim of this thesis was to describe the social structure of a dynamic sow herd and identify key animals using social network analysis. The novel outcomes of the thesis reveal that despite a lack of linear hierarchy, there is social inequality within the herd, that consistently

include key individuals with greater prominence and influence than their conspecifics. By differentiating sows concerning the social role, it became possible to evaluate differences in behaviour and reproduction, by examining changes over three production cycles, the stability of behaviour was determined. Although there was a general temporal instability of behaviour at an individual level between production cycles, at a group level, the overall social structure remained consistent. SPS and SIS are dispersed throughout the herd with variable levels of connectedness; this provides a new perspective on which individuals might affect the herd. The results and findings provide valuable insight into the behavioural strategies sows are implementing in response to an unstable social environment, with context-dependent behaviour occurring in both the preferential association and agonistic networks. Predictive behaviour is pivotal for informing management strategies, and this work indicates the difficulties that may arise from forming judgements of individual behaviour or personality from the traditional tests. This study revealed another novel finding relating to the stability of betweenness centrality in the aggression networks, demonstrating an ultimate measure of behaviour that is potentially more reliable and unaffected by a changing social environment. A fresh approach considered the relationship between social roles and reproductive performance. It is established that a link exists in other species between positive behaviours, enhanced reproduction, and offspring survival. The evidence from this thesis provides additional knowledge and understanding to suggest a link may also exist between preferential associations and stillborn piglets in gestating sows. It supports the continued obligation to evaluate management strategies based upon positive behaviours in commercial species. The findings made available are an enlightened insight; stillbirths represent principal

welfare and economic issues in the commercial farming industry and demonstrate future research can only extend the novel results of this work.

Glossary of terms and abbreviations

Arc reciprocity: Arc reciprocity counts the number of arcs (directed edges) and calculates the proportion of arcs that are reciprocated. The method includes the number of reciprocated arcs divided by the total number of arcs.

Asymmetric dyad: Where A interacts with B, but B does not reciprocate the interaction.

Attribute: Attribute data refers to the genotypic or phenotypic individual variables such as parity.

Betweenness Centrality: A measure of the number of times a node falls along the shortest path between two previously unconnected nodes.

Brokerage: Relates to closing structural holes within a network. A broker can transfer information, behaviour, or disease between previously unconnected individuals, effectively acting as a conduit. It is the only mechanism through which information, behaviour or disease can be transferred to isolated or unconnected nodes.

Brokerage typology: Divide's brokerage into five categories to show how information, behaviour or disease may be transferred within and between subgroups. The categories include coordinators, gatekeepers, representatives, consultants, and liaisons.

Census count: The frequency of specific brokerage typologies (coordinators, gatekeepers, consultants, representatives, and liaisons) that are occurring within a network.

Centralisation: The extent to which a single node dominates a network.

Clustering coefficient: The extent to which there is the formation of triads in a network, it reflects if friends of friends will become friends and are referred to as transitivity or clumpiness.

Cohesion: Relates to the connectedness of a network

Complete network: A network in which nodes have unrestricted access to each other.

Component: A set of connected nodes in which every node can reach every node by some path (there are no structural holes).

Connectedness: The proportion of nodes present within a component or subgroup.

Consultant: Brokers the transmission of information, behaviour, or disease between two previously unconnected nodes. Unconnected nodes belong to the same subgroup as each other but to a different subgroup than the consultant.

Coordinator: Brokers the transmission of information, behaviour, or disease between two previously unconnected nodes within its subgroup.

Degree centrality: The number of ties a node has within a network. In this study, it refers to the number of preferential associations or agonistic interactions.

Density: The number of ties within a network proportionate to the total potential number of ties.

Directed network: Shows the direction of an initiated tie between two nodes, allowing for visualisation of the initiator and recipient of the interaction.

Edge: Is the connection between two nodes, also referred to as a tie.

E-I Index: The external-internal index evaluates the extent to which individuals are assorting by trait, measuring potential homophily and heterophily occurring within a network.

Gatekeeper: Brokers the transmission of information, behaviour, or disease between two previously individuals. One belonging to the same subgroup as the gatekeeper and another belonging to a different subgroup.

Indegree centrality: The number of ties a node receives. In this study, it refers to the number of preferential associations or agonistic interactions a sow receives.

Initiated ties: The total number of behavioural interactions an individual instigates, also referred to the outdegree centrality. In this study the initiated ties are the total number of preferential associations or aggression that an individual instigated.

Isolate: A node that is not connected to any other node in a network.

***K*-core**: A subgraph or subgroup in which every node has degree *k* or more connections with other nodes within the *k*-core.

Liaison: Brokers the transmission of information, behaviour, or disease between two previously unconnected nodes. Previously unconnected nodes belong to different subgroups than each other and different subgroups as the liaison.

Network: Shows the connections of individuals within the same social group or system.

Node: The individuals or entities within a network; in this study, nodes refer to individual sows.

Normalised relative brokerage: The brokerage typology that is more significant to an individual.

Null dyad: A dyad where there are no ties or relationship between two nodes.

One-mode network: A network comprising of nodes that are like each other.

Outdegree centrality: The number of initiated ties a node makes. In this study, that refers to the number of preferential associations or agonistic interactions a sow' initiates.

Received ties: The total number of behavioural interactions an individual receives, also referred to the indegree centrality. In this study the received ties are the total number of preferential associations or aggression that an individual experienced.

Reciprocity: In a directed network, it shows the extent of reciprocated ties between two nodes.

Representative: Brokers the transmission of information, behaviour, or disease between two previously unconnected nodes. Representatives broker in the same way as a gatekeeper, however,

the flow direction of what is being transferred is different, allowing the representative to represent their subgroup with a different subgroup.

Socially influential sows (SIS): Refers to socially influential sows which have a significantly higher betweenness centrality than their subgroup conspecifics.

Sociogram: A visual representation of a social network.

Spring embedding: Refers to the graphical layout algorithm which determines the layout of a sociogram through optimising the visual aesthetics of the graph.

Socially prominent sows (SPS): Refers to socially prominent sows which have a significantly higher degree centrality than their subgroup conspecifics.

Structural hole: A gap in a network in which previously unconnected nodes are prevented by interacting with each other.

Symmetric dyad: A dyad where A and B interact with each other.

Ties: Shows the connection between two nodes, also referred to as an edge.

Transitivity: The extent to which two nodes are connected will impact the development of a tie third node, to whom they are also connected, creating triadic closure.

Undirected network: Does not show the direction of interaction, visualisation of the initiator and recipient of interaction is unknown.

Unweighted network: Contains only binary data relating to the interactions between nodes and does not show the total frequency of ties.

Weighted network: Provides the total frequency of ties between nodes.

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